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No. 1. — *Contributions to the Morphology of the Turbellaria.* — I. *On the Structure of Phagocata gracilis, Leidy.* By W. M. Woodworth.[1]

In the fall of 1887, Mr. H E. Valentine of West Somerville, Mass., brought to the Embryological Laboratory of Harvard College some planarians, with the suggestion that they might be infested with parasites. The planarian proved to be the interesting Phagocata gracilis of Leidy, and the supposed parasites were the pharynges of the complicated digestive apparatus. At the suggestion of my instructor, Dr. E. L. Mark, I undertook the study of this curious Triclad.

The animal, which was afterwards named by Leidy Phagocata gracilis, was first described by S. S. Haldeman ('40, p. 3) in 1840, under the name of Planaria gracilis: "Body oblong, suddenly tapering to a point posteriorly: sides nearly parallel; head square in front, with a projecting appendage on each side: neck narrowed; eyes (two) situated on each side of the narrower part; these are oblong and white, with a black dot at their internal side: ventral opening less than one third the entire length from the posterior extremity, and from this opening an intestine is sometimes protruded. General color fuliginous, veined with black. Length, $\frac{3}{4}$ in., breadth, $\frac{1}{10}$. Hab. springs in Eastern Pennsylvania."

In 1848, Leidy published a further description of the species, giving to it the name of Phagocata ('48, p. 248), because, as he says, "I detected such a remarkable peculiarity in the digestive apparatus as led me to investigate its anatomy in detail, and to form for it a separate sub-genus, characterized as follows: —

"*Phagocata*, oblonga, plano-convexa, nuda, contractilis, mucosa, antica auricularia. Aperturæ duæ, ventrales, ad os et ad generationem pertinens. Proboscides multæ.

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXIV.

No XXIII. of these Contributions appeared in the Proceedings of the American Academy of Arts and Sciences, Vol. XXV., under the title, "Preliminary Notice on Budding in Bryozoa." By C. B. Davenport.

"*P. gracilis*, nigricans, lateribus parallelis, postero acuto abrupte, plerumque antico recto; oculis duobus. Long. 9 lin., lat. 1 lin. Habitat in fontis Pennsylvaniæ.

"*Description.* Oblong, limaceform, naked, convex superiorly, flat inferiorly, very contractile; sides ordinarily parallel, convex when the animal is in a contracted state, convergent anteriorly when elongated; anterior extremity with a lateral triangular auricular appendage, straight in front, by contraction becoming convex or concave; posterior extremity abruptly pointed; ocelli two, anterior, composed of an oblong, semi-transparent (nervous?) mass with an intensely black dot of pigmentum at the internal posterior part; ventral apertures two; oral aperture a little less than one third the length of the body from the posterior extremity. Color black or iron gray, and in some younger specimens latericeous."

I have quoted Leidy's description in full, because it seems to me that the first description of so striking and aberrant a species is of uncommon interest.

It is noteworthy, that, notwithstanding the faithfulness of the description, and the remarkable peculiarities of the worm, no mention of the species has been made for over forty years. It is also strange that Girard should have been ignorant of the existence of Leidy's paper, for in his list of North American fresh-water Planariæ ('51, p. 264) he uses the name proposed by Haldeman, "Planaria gracilis," and says that it is "common about Cambridge in pools and rivulets." He adds, in a note, "Planaria gracilis and very likely Planaria tigrina will not remain in the genus Planaria as soon as we shall know their internal structure." In a subsequent paper ('51[a], p. 2), "Die Planarien und Nemertinen Nord-Amerikas," the species is described under the name given to it by Leidy, but no mention is made of the most striking characteristic discovered by that observer, — the multiplicity of the pharynges.

The structural peculiarities of Phagocata were not simply ignored, they were even denied by no less an authority than von Siebold, who explained the "proboscides" of Leidy as so many processes from the lip of one normal pharynx. After quoting the description, he says ('50, p. 389): "Das erwachsene Thier soll 23 Rüssel haben, die es beim Fressen alle hervorstreckt; Ref. vermuthet, dass der Rüssel eine trichterförmige ausgezackte Mündung besitzt, und dass die beweglichen Fortsätze des Rüsselrandes für ebenso viele einzelne Rüssel gehalten worden sind."

Diesing, like von Siebold, was incredulous; in his "System," he says ('50, p. 207), "Œsophagus protractilis multi partitus (proboscides multæ Leidy)." Twelve years later, in the "Revision der Turbellarien," he writes ('62, p. 506), "œsophago multipartito."

Stimpson ('58, p. 23) in his Prodromus apparently followed Diesin for he says "œsophago protractili multipartito."

Recently, Professor Leidy ('85, p. 49) has figured Phagocata gracilis in a popular account of "Planarians." These are the only descriptions of Phagocata I have been able to find.

Phagocata gracilis, Leidy.

When viewed from above, the general form of the animal is elongated; its lateral margins are nearly parallel, being slightly convex posteriorly; the widest part of the body is in the pharyngeal region. The largest specimens measure 30 mm. in length by 4½ mm. in breadth. Anteriorly the sides converge slightly up to about the region of the eyes, where the diameter increases, thus forming the so called head. This bears the lateral auriculate appendages. The lateral appendages are rounded, rather than triangular as described by Leidy; they are continuous with, and in fact form part of, the anterior extremity; posteriorly, the sides converge to a point (Fig. 20 *a*). The eyes appear as two elongated oval white spots, with black pigment on the internal edge. They are situated on the narrow part or "neck."

Haldeman and Leidy have described the head as being "straight in front." This appearance is seen only when the animal is at rest. It is then much contracted in the direction of its antero-posterior axis, and is usually much distorted; at such times it often appears as a shapeless black lump, this condition probably being a means of protection (Figs. 20 *b* and 20 *c*). When in motion the anterior extremity is usually convex, but not always, for it may be straight, sinuous, or concave; these shapes are only temporary, following each other in quick succession. The head changes its form especially when the animal approaches some object; for this part of the body is functional as an organ of touch; that it is suited structurally to be a kind of feeler will be evident from the description of the nervous system which follows.

Phagocata gracilis has a shiny black appearance when viewed by reflected light, but by transmitted light it is of a greenish gray color. The color may vary from black to a reddish brown on the one hand, or to a light gray on the other. I have seen small specimens which were

almost milky white. The ventral surface is of lighter color than the dorsal, and there are light areas about the ventral apertures. The pigment is densest in the dorsal median line, where it forms a dark band; it diminishes toward the sides of the animal, the edges of which are quite destitute of it. The distribution of the pigment in the head region presents many variations. In most cases the posterior borders of the auriculate appendages show two light spots, and there is a third one, somewhat triangular in shape, at the anterior end in the middle line. The marginal area of the head, like that of the body, is free from pigment. Sometimes the whole head region is light with the exception of the middle line between the eye spots, where there is an extension of the dark median band previously referred to. Light non-pigmented areas occur wherever there has been a reparation of the tissues resulting from injury.

By an examination of the animal in the natural condition, only a few of the internal structures can be identified, because of the large amount of pigment present. When viewed from above, the most striking feature is a large oblong light region, the pharyngeal cavity with its contained pharynges. Immediately behind this a similar but smaller spot marks the position of the penis. From the ventral side the nervous system may be dimly seen as two long whitish bands united by transverse commissures and coming together in the head region in a bilobed enlargement, the brain. Leidy apparently confused these structures with the excretory organs, no trace of which can be seen on the living animal. He says ('48, p. 250): "There appears to be nothing peculiar about the arrangement of the blood-vessels, if such they be: the term being applied to two semi-transparent lines passing along each side of the ventral surface, and a third along the middle of the dorsal surface, the three freely communicating with each other by transverse lines and numerous smaller branches, the whole forming an extensive reticulation upon the surface of the body. At the anterior part of each ventral line, I distinctly observed a dilatation to exist." And again: "I could detect no traces of a nervous system." The two "semi-transparent lines" are without doubt the longitudinal nerve trunks, and the "dilatations at the anterior part of each," the lateral enlargements of the brain. What he means by the "third" line "along the dorsal surface," I cannot say. When sexually mature individuals are subjected to pressure, parts of the vasa deferentia and oviducts can also be made out.

Phagocata differs from all other Triclads in possessing many pharyngeal tubes instead of one. All the pharynges lie in a common chamber,

and when protruded reach the exterior through a single orifice, but they open into the intestinal cavity separately. One of these pharynges, like the single pharynx of other Triclads, joins the intestine at the junction of its main trunks; the others are connected with the inferior median surface of the lateral trunks (Plate II. Fig. 20). The odd median pharynx is largest, and therefore most prominent of all. The others, which arise from the intestine farther back, are successively shorter, as well as narrower, the more remote they are from the median proboscis. The attachment of the smallest ones is about as far from the posterior end of the animal as the attachment of the chief one is from its anterior end, so that the chamber which they all occupy embraces the middle half of the body. Although there are about as many pharynges attached to one of the lateral trunks of the intestine as to the other, they are not arranged in pairs, nor have their positions any definite relation to the side branches of the intestine which open into the lateral trunks. The pharynges are rather less numerous than the side branches; they sometimes arise opposite to a branch, sometimes opposite to a space midway between two branches, or at other intermediate points. The foremost of the lateral pharynges is often considerably in advance of the corresponding proboscis of the opposite side of the body (Fig. 20). Leidy ('48, p. 249) has well described the appearance and action of the pharynges in the living animal. He says: "They are considerably longer, but narrower, than in *P. lactea*, and when not in use are packed together within the animal, so that, when the latter is placed beneath the microscope and slightly compressed, they will be seen pressing upon one another in such a manner that, if one changes its position, it will be instantly occupied by another. Those which are formed last are smallest, but they soon gain their full size. If one of these animals be punctured or cut, one or more of the proboscides will be instantly protruded as if they existed under pressure, and will move about in all directions, appearing as if entirely without the control of the animal; or if one of the animals be crushed between two slips of glass so that the proboscides will be torn from their attachment, they move about involuntarily, always in a line forwards or towards the mouth. . . . In this progressive course they constantly contract and dilate; the mouth opens, and any matter in its vicinity rushes in, when it is closed and the matter passes onwards, and by the alternate contraction and dilatation of different parts of the same tube it is thrown backwards and forwards several times, and finally violently expelled at the torn extremity. When they have escaped from the

ruptures of the tegument produced by crushing, or when snipped off with a pair of scissors whilst the animal is feeding, they will present the same curious phenomena. In fact, these curious independent movements caused me at first to mistake the organs for viviparous young, and it was not until I had frequently observed the animal feeding, and examined its structure beneath the microscope, after having fed them upon colored food, that I was convinced of their true nature."

It was these automatic movements of the detached pharynges that at first led me also to believe that they were parasites. They appear as long, white worm-like bodies, one end being truncated, the other ragged and uneven, where it was torn from its attachment. They move about quite rapidly by means of the cilia with which they are covered, and waves of contraction continually pass along the length of the tube from the truncated to the ragged end. The mouth end may be greatly expanded so as to form a funnel-like structure, or it may be so contracted as to obliterate the lumen. I did not succeed in satisfying myself of the real nature of these structures until I examined one of the animals while it was feeding. I placed one of the Lumbriculidæ in a watch-glass with a Phagocata, which soon attached itself to the annelid by throwing out its many pharynges, some of which were wrapped about the victim, while others were thrust into its body (Plate II. Fig. 13). The soft parts of the prey were rapidly sucked up and swallowed by means of the peristaltic motions of the pharynges, so that in a short time there was left nothing but the empty and shrivelled integument.

By far the best reagent for killing is hot corrosive sublimate. An excess of the salt is added to the saturated aqueous solution and the whole is heated to the boiling point. A very strong solution can be prepared in this way, as the salt is more soluble in hot water than in cold. Kennel ('88, p. 455) has recommended the use of 50% nitric acid. I have used with entire success a modification of his method, viz. a cold saturated solution of corrosive sublimate in 50% nitric acid. The worm is placed on a plate in as little water as possible, and when properly extended the fluid is quickly poured over it. After a few minutes' immersion the fluid is replaced by a saturated aqueous solution of corrosive sublimate, in which the worms remain for half an hour and are then washed. I know of nothing else that will kill so quickly, and at the same time leave the tissues uninjured. For the study of the intestinal tract, unstained specimens were cleared in clove oil. The amount of pigment so obscures the organs lying beneath, that the ramifications of the intestine could be

traced only on cleared specimens in which the intestine contained dark-colored food matter. For staining, Grenacher's alcoholic borax carmine followed by differentiation with acid alcohol proved to be the most useful and reliable method. I have stained both *in toto* and on the slide. Good sections for topographical study were obtained by staining in alcoholic borax carmine for 24 hours and cutting in the horizontal plane sections 30 μ in thickness. By thus lightly staining, the nerve tissue takes none of the color, and in such comparatively thick sections the finer branches show as white lines against a red background. Orth's picrocarminate of lithium is a valuable reagent on account of the selective action of the picric acid for all glandular tissue, which it brings out in sharp contrast to the red color of the other tissues. I have used this reagent also with excellent results for macerating. The affinity of hæmatoxylin stains for formed substances renders them of little use; their intense reaction with the great number of glandular structures tends to obscure results. For isolation preparations, the best results were obtained by macerating directly in the stain. I also used successfully the osmic-acetic method of maceration on fresh material. The isolated living pharynges were killed in hot 1% silver nitrate for the purpose of demonstrating the epithelium. Depigmenting was accomplished by the use of a 1% solution of potassic hydrate which was allowed to act for a few minutes on sections fixed to the slide with Schällibaum's clove-oil collodion fixative.

Cilia are present over the whole surface of the animal. In material that had been prepared in hot corrosive sublimate, the middle region of the ventral surface, where the hypodermis is thinnest, was often destitute of cilia. Likewise at the lateral edges they may be wanting. These conditions are, however, due to the action of the reagent, since in the living animal cilia are always present in these places. At the anterior end of the body on either side of the head, the cilia are somewhat longer than elsewhere. They attain their greatest length at that portion of the margin of the head which forms the auriculate projections. From the middle of each projection they gradually diminish in length until, at the anterior tip of the body and at an equally distant point behind the auricles, they are reduced to the normal length. These two areas covered by the longer cilia probably correspond to the "Tastorgane" of Iijima ('84, p. 366), and are directly related to local modifications of the hypodermis.

I cannot find either the short immovable hairs or the long "Geissel-

haare" seen by Iijima in other Triclads at the anterior margin midway between the areas of the "Tastorgane"; nor have I found in Phagocata that the cilia in the head region move in different directions, as Minot ('77, p. 407) has observed in the case of other fresh-water planarians.

There has been a difference of opinion among writers as to the possibility of certain regions of the body being normally destitute of cilia. Metschnikow ('66, p. 436) and Kennel ('79, p. 125) found cilia covering the whole surface in Rhynchodesmus and Geodesmus, but Zacharias ('88, p. 542) states that the dorsal surface of a variety of Geodesmus is bare, and Vejdovsky ('90, p. 132) maintains the same for Microplana, the cilia in the latter cases being confined to the ventral surface or sole. It seems to me, however, that Moseley ('74, p. 118) long ago offered a satisfactory explanation of the condition, by saying that in Bipalium the cilia on the dorsal surface of land planarians, being weaker through comparative lack of function, are consequently more easily destroyed by the action of the reagents used in the preparation of the material. Considering the habits of land planarians, and especially the dissimilar conditions to which the dorsal and ventral surfaces are subjected in regard to moisture, exposure, contact, etc., it is not strange that the conditions of the cilia of the different surfaces should be unlike. Iijima ('84, p. 366) states that it is the exception for the edges of Dendrocœlum lacteum to be ciliated, and that the almost constant absence of cilia is due to certain parasites (Trichodina). He also speaks of a species of Geoplana from South America in which the cilia of the dorsum are replaced by a granular crust. I believe that in planarians there is primarily no localization of the cilia, and that all non-ciliate conditions are secondary.

I could nowhere find a *cuticula*. The superficial portion of the cells of the hypodermis takes a somewhat deeper stain than the body of the cells, but there is no sharp line of demarcation between the two; the color of the superficial portion fades gradually into that of the body of the cell. A true cuticula such as that described by Minot ('77, p. 407) and Loman ('87, p. 69) for Triclads, and by Keferstein ('68, p. 16) for Eurylepta, is wanting, and there is only a thickening, a condensation, of the superficial plasma of the hypodermal cells.

The *hypodermis* has proved to be the most difficult of the tissues to study, because of the minuteness of its elements, and the enormous number of dermal rods, or rhabditi, which so obscure the true conditions that it is only after long and patient study of thin sections and of

macerated material that one can learn what the true characters of this tissue are.

The hypodermis is thickest on the dorsal surface; it becomes thinner toward the edges of the body, and in passing around to the ventral surface it still continues to become thinner as far as the middle line, where, forming part of the floor of the pharyngeal cavity, it reaches its greatest attenuation. There are hypodermal thickenings around the oral and genital openings, and also over two sensory areas on the ventral surface of the head region, which will be described in another place.

It is almost impossible to find a region where the cells of the hypodermis are not modified by the presence of the dermal rods. In order to get at the natural appearance of the cells, it is necessary therefore to study them in young specimens, and in the region where the rods are fewest; this region I have found to be near the margin, on the dorsal side. Very thin cross sections of young individuals are the most favorable ones for this purpose.

The cells are columnar, the height necessarily varying with the thickness of the hypodermis. The nuclei are large, have an irregular or sinuous outline, and are situated, as a rule, near the bases of the cells (Figs. 1 and 2). This position is not constant, and depends upon the number and influence of the rhabditi that are present. There is no nucleolus proper, the chromatin being scattered through the nucleus in many large granules. The size of the nucleus does not appear to depend upon the size of the cells; for while the cells in different regions vary to a great extent, the nuclei remain of nearly uniform size.

The cells are finely striated; the striations are most prominent at the basal ends of the cells, and cannot be traced to their free ends. Such radial striations have been described by Böhmig ('86, p. 294) in the hypodermis of Graffilla, and more recently by Lippitsch ('90, p. 328) in the epidermal cells of Derostomum. Iijima ('84, p. 369) also alludes to fine striations in the epidermal cells of Planaria polychroa. The cells do not "etwa flach auf die Basalmembran aufsitzen," but are connected with it by fine processes "welche etwa kammförmig ziemlich dicht neben einander stehen." These processes he believes to be directly continuous with the striations of the cells, and to be protoplasmic prolongations of the cells. He traces them through the basement membrane into the muscles below, thus establishing "eine organische Verbindung zwischen dem Epithel und den Körperinnern." His figure (Taf. XX. Fig. 4) is confusing, and in addition was drawn, as he admits, from specimen in which the basement membrane exhibited pathological con-

ditions. Besides the striations in the cells, there appear creases or folds resulting from the pressure of the rhabditi.

In thick sections through regions where the rhabditi are numerous, the epidermal cells have the appearance of being joined to the basement membrane by foot-like processes. This appearance at first led me to believe in a condition like that described by Iijima, and it was only after studying sections of material in which the rhabditi had been removed (Fig. 3) that I understood their relations to the cells.

The rhabditi do not lie *in* the hypodermal cells, but *between* them. Kennel ('79, p. 126) and Braun ('81, p. 305) are the only observers who have described them as having an *inter*cellular position. It will be seen from the following description of their development in Phagocata, that such a position is the only natural one. The presence of these rods between the cells produces a crowding, and the pressure is so great that it causes the cells to become displaced and much modified in shape. The nuclei may be pushed out to the free ends of the cells, or crowded down to their bases, and the cells themselves may be so reduced as to appear like mere filaments (Fig. 3). Kennel ('79, p. 126) describes the epidermal cells of Rhynchodesmus after the removal of the rhabditi, as "feine Fädchen . . . so lang als die Epidermis dick ist." Regarding their intercellular position, Braun ('81, p. 305) states for Bothrioplana that the rhabditi "nicht allein zwischen den Zellen stehen, sondern auch das Protoplasma der Zellen durchbohren." In Phagocata, as in Rhynchodesmus, the rhabditi are so numerous that the hypodermis appears at first to be entirely composed of them. As Kennel expresses it, "ausser den feinen, fadenförmigen Zellen kaum etwas anderes Platz zwischen ihnen hat." It is in thick sections, where the epidermis is many layers deep, that the bases of these compressed cells present an appearance as if the hypodermis were connected with the basement membrane by fine foot-like processes. This appearance is only seen where the rhabditi are most numerous. At the lateral edges of the body, where there are few, and where consequently the cells retain their primitive cylindrical form (Fig. 2), the latter are applied to the membrane by their broad bases. It is in these regions also that the striations previously spoken of are most distinctly seen.

Moseley ('74, p. 118) says, "The epidermis here [land planarians] is seen to be made up of large gland-cells and cells containing rod-like bodies and a certain amount of vertical filaments." "The irregular filaments which fill up the interspaces between the gland-cells and rod-like bodies appear to be the remains of the cell-walls and rod-like bodies."

He further says, "The substance of the epidermis is probably made up, in the living condition, of cells resembling the gland-cells described, but of various dimensions, and of cells containing rod-like bodies."

Since the "rod-like bodies," or rhabditi, are really modified glands, Moseley's statement amounts to saying that the epidermis is composed entirely of gland cells, a conclusion which it is not easy to adopt. Moreover, I believe that Moseley's "gland-cells" are only rhabditi that have been modified by the action of the reagent which he used for their demonstration. Kennel ('79, p. 126) obtained similar conditions by the action of chromic and acetic acids on the rhabditi of land planarians. I have found that in Phagocata by the use of picric acid the dermal rods become swollen and granular, resembling the "gland-cells" described and figured by Moseley. "The vertical filaments" were undoubtedly the true epidermal cells, reduced to a filamentous condition by the influence of the many rhabditi lying between them.

I cannot find any organic connection between the cells of the hypodermis and the deeper tissues, such as has been described by Iijima. Although appearances like those described by him do occur, they are secondary conditions, dependent on the presence of the rhabditi and the development of their mother cells. The basement membrane is everywhere traversed by fine tubular processes of the mother cells of the rhabditi, which lie imbedded in the body parenchyma. This fact, together with striations of the cells of the hypodermis and the ultimate reduction of these cells to filaments, might easily lead to conclusions such as those of Iijima. His sections were thick (10–20 μ) both absolutely and in proportion to the length of his largest specimens (20 mm.), whereas my sections were only 5–10 μ in thickness, although the worm attains the length of 35 mm.; moreover, isolation preparations were studied in connection with these sections.

The hypodermis consists of the hypodermal cells and the rhabditi that lie between them. There are no unicellular glands in it. Lang ('84, p. 49) described in Polyclads a granular "interstitial tissue" containing nuclei and pigment which arises, according to his conjecture, from a coalescence of indifferent epithelial cells. Such conditions I cannot find, nor can I detect any cement ("Kittsubstance"), such as that described by Graff ('82, p. 44) for Rhabdocœles.

The dermal rods or *rhabditi* are defined by Graff ('82, p. 49) as "die stark lichtbrechende glasartige homogenen Stäbchen, welche weder einen Faden noch einen Nadel einschliessen und durch ihre glatte Oberfläche, regelmässige Gestalt und ihren Glanz auffallen."

In Phagocata the rhabditi are found in almost every portion of the hypodermis, there being only one region from which they are altogether absent, viz. around the gonopore, where they are gradually replaced by many subcutaneous glands, which open to the exterior in a broad circular area surrounding that orifice. They are present around the oral opening, even up to the aperture, where they abruptly cease. They are most abundant in the middle line on the back, becoming gradually fewer toward the sides and anterior end, but they are again abundant on the ventral surface. They are found over the eyes, and in the epithelium of the two anterior sense organs, where they are well developed but few in number. Iijima ('84, p. 371) has stated that they are wanting in this region in the case of D. lacteum, but are present in Planocera polychroa and Polycelis tenuis. He has also shown that in the case of D. lacteum they are unusually abundant in the region of the genital orifice, both in the epithelium and in the parenchyma, and supposes that they have a sexual significance as urticating organs, the "Liebesfeile" of Schneider; but their absence in this region in Phagocata precludes the assumption that they have in this species any such function.

The rhabditi are all of one kind, but they vary in size. The variations are not local, different sizes occurring wherever rhabditi are found. Some are as long as the hypodermis cells, while others are comparatively short; they vary from 1.5 μ to 16 μ in length. There is an interesting correlation between the thickness of the hypodermal layer and the size of the largest rhabditi; those of the thin hypodermis of the ventral surface are invariably smaller than those of the dorsal side. Each is spindle-shaped, and the outer end is slightly more pointed than the deep end. They stain intensely in the carmine dyes, and then appear perfectly homogeneous; but when stained in Orth's picrocarminate of lithium with an excess of the picric acid, they take on a bright yellow color, and appear more or less swollen and distorted, according to the length of time the dye is allowed to act. Often they have the appearance of hollow capsules filled with granules, or containing a few irregular refractive lumps (Fig. 9). It was probably the swollen and altered rhabditi that Moseley mistook for gland cells. The peripheral portion of the substance of the rhabditi is not affected by the reagent as the contents are. This outward unaltered portion presents the appearance of a capsule, or thick membrane, with a double contour. Moseley says of his glandcells, "The cell appears to have a double wall, for an irregular crumpled membrane is seen often within it."

The rhabditi which lie between the hypodermal cells are not parallel, but are somewhat inclined toward each other, the outer ends generally converging about centres so as to form groups or packets. The small ones lie out near the free surface of the hypodermis; and the largest may reach the basement membrane (Fig. 1). Usually the long axes of the rhabditi are approximately perpendicular to the surface of the epidermis, but they may assume almost any angle with each other; small rods are sometimes seen lying at right angles to neighboring ones.

It was first shown by Oscar Schmidt ('48, p. 6), in 1848, that in the case of Rhabdocœles the rhabditi are developed in subcutaneous flask-shaped cells. Since that time similar conditions have been discovered in all the Triclads. Up to the present time, the development of these cells, "Stäbchenbildungszellen," has not been traced. My studies seem to throw some light on their genesis, and also to show how the rods find their way out between the cells of the epidermis. I first recognized the parent cells in isolation preparations, and saw them in sections only after depigmenting and staining the sections on the slide. Later, I obtained a fresh supply of material, and was able to demonstrate them in abundance, and in all stages of development. They are more easily to be seen on the ventral side of the animal, where they are less obscured by pigment. In their fully developed condition they lie in the body parenchyma immediately beneath the longitudinal muscles. On the ventral side, where the muscle layer is very thick, they may be found in between the strands of the muscles as well as below them. The parent cells have the form of flasks with greatly elongated narrow necks tapering off into long tubular processes, which are traceable outward through the muscles to the basement membrane, and, traversing this, are seen to open out between the cells of the hypodermis. Thus the deep-lying parent cells are in direct communication with the outer world (Figs. 1, 6, and 10). It is by means of these tubular processes that the rhabditi find their way to the exterior, and at length come to occupy positions between the hypodermal cells. I have previously pointed out that the rhabditi in the epidermis lie in groups or packets; presumably each of these groups was at one time contained in a single parent cell.

The connection of the parent cells with the epidermis is a primitive one, for they are only modified cells of the hypodermis, which never cease to retain their connection with that layer. In the earliest stages of development that I have found, they appear like small sacs imbedded in the superficial portion of the longitudinal muscle band, close

to the basement membrane, with which they are connected by short necks or tubes (Fig. 4). The cell at this stage contains a single very large nucleus, in which there is no nucleolus, since the chromatin exists, as in the other cells of the hypodermis, in the form of fine particles scattered uniformly through the nucleus. Later, the cell begins to sink deeper into the tissue below the hypodermis, and the tubular neck increases correspondingly in length. The cell contents become finely granular, and appear to grow at the expense of the nucleus, which no longer fills so completely the sac, but becomes smaller and occupies the bottom of the cell (Fig. 7). In the protoplasm surrounding the nucleus, there appear small, round, highly refractive particles that stain deeply. These increase in number and in size, and soon become elongated, taking on the spindle shape so characteristic of the rhabditi (Fig. 6, *rhb.*). During these stages of formation the cell comes to lie in the body parenchyma below the muscle bands, but still retains a connection with the hypodermis by means of its long tubular process. The cells are at length filled with rods, and the nucleus is crowded to the bottom of the cell (Figs. 1, 5, and 10).

The fully developed rods are guided to the exterior by means of the tubular prolongations of the parent cell, and finally make their way through the basement membrane and come to lie between the cells of the hypodermis. The rhabditi, so long as they are contained in the parent cell, are not hard and rigid, but possess a certain amount of plasticity, as can be seen by the manner in which they are bent when many are packed in one cell. This plastic condition of the rods facilitates their passage through the basement membrane. I have been able to find a number of cases such as that represented in Figure 8, where I have shown one of the rods in the act of passing through the membrane. The rods possess this pliability until they leave the deeper tissues, and they attain their definite shape only after they reach the hypodermis, where they become hard and inflexible. After the discharge of the rhabditi, the parent cells become absorbed and disappear.

Anton Schneider ('73, p. 87) says concerning the parent cells, "Sie haben mehrere nach der Haut gehende Ausläufer, deren Epithelzellen reichlich damit gefüllt sind." According to Moseley ('74, p. 119), "The parent cells of the rod-like bodies are arranged beneath the external longitudinal muscular layer at a tolerably even depth; they are, in spirit specimens, of an elongated oval form, with the upper extremity drawn out in a point or long filament, which in some cases may be seen to reach up to the basement membrane." In another place ('74, p. 120)

he says, "On treatment with potash, the cells of Bipalium swell up, are seen to contain rod-like bodies, and the fine filament at the upper extremity appears like a duct leading to the surface of the basement membrane."

Hallez and Iijima do not make mention of any processes of the sub-hypodermal parent cells, but believe that the cells are ruptured, and that the rhabditi make their way to the epidermis through the tissues of the body. Hallez ('79, p. 6) says: "Jai été temoin une seule fois de la rupture d'une cellule productrice chez Mesostomum tetragonum; il m'a été impossible de retrouver dans cette cellule rompue la moindre trace du noyau." Iijima ('84, p. 371) writes as follows: "Die Bildungszellen sind rundlich und mit einem ausserordentlich feinkörnigen Inhalt versehen." And again: "Haben die Rhabditen ihre definitive Grösse erreicht, so durchbrechen sie die Zellenwand, welche schlieslich absorbirt zu werden scheint und wandern durch den Bindgewebe und die Basalmembran entweder einzeln oder in Gruppen nach aussen in die Epidermiszellen, in denen sie definitiv verbleiben."

Not all of the rhabditi that are developed in the parent cells of the sub-hypodermal tissue find their way to the exterior. Many of the cells apparently lose their connection with the hypodermis, and their rhabditi are discharged into the body parenchyma; only on this assumption can one explain the presence of the numerous rhabditi that are found scattered in the sub-hypodermal tissues. This condition is not the normal, or at least not the original one. These often occur in large numbers in the zone immediately inside of the longitudinal muscle bands, which is occupied by the mother cells, where they lie in no definite positions, and with their axes directed at all angles.

Rhabditi of all sizes may be developed in the same parent cell. Those of different sizes are not confined to special cells, as found by Schneider ('73, p. 83) and Graff ('74, p. 128) for Mesostomum. Besides the fully developed rhabditi there are in the cells particles that have no constant form, but have the same optical appearance and stain the same as the rhabditi (Figs. 6, 10). These bodies may be either residual matter, disintegrating rhabditi, or incipient rods. They never occur in the epidermis, but are left behind after the discharge of the rhabditi, and by the absorption of the wall of the parent cell they find their way into the body parenchyma, where, with the rods previously referred to, they lie scattered about. Lang ('84, p. 52) found similar bodies along with the rhabditi in Polyclads, and speaks of them as "junge kugelige Stäbchen." I am inclined to regard them as residua secretions.

To my mind it is unquestionable that the parent cells of the rhabditi are of ectodermic origin, as first suggested by Hallez ('79, p. 7). It is only in Triclads and in Rhabdocœls that the mother cells lie in the deeper tissues, and we know so little about the embryology of these groups that we cannot tell just how the passage from the exterior takes place. I have endeavored to show that the cells have a connection with the hypodermis in the earliest stages of their development, long before they show any traces of rhabditi, but whether the cells pass from the hypodermis through the basement membrane, or are separated from the hypodermis before the formation of such a structure, I cannot say. The epidermis of embryos of Mesostomum was found by Graff ('82, p. 56) to be filled with rhabditi, while he could find no traces of the sub-hypodermal parent cells so prominent and abundant in the adult. In Polyclads, the development of the rhabditi is in my opinion identical with that in Triclads; but in the former the parent cells lie permanently in the hypodermis, whereas in the latter they sink down below that layer, where greater opportunity for growth is afforded. The condition found in Polyclads, therefore, I believe to be the primitive one.

Another mode of origin of the parent cells of the rhabditi has been proposed by Loman ('87, p. 69), who considers them to be modified connective-tissue cells that migrate from their original positions in the mesenchyma and pass bodily through the basement membrane, and come to lie eventually between the cells of the hypodermis; or, in the words of the author, "Nach meiner Meinung sind die Stäbchenzellen mesenchymatöse Gebilde, die eine factische Wanderung durch dass sie umgebende Bindgewebe unternehmen, während ihr Inhalt sich zu den fadenförmigen Stäbchen ausbildet. Endlich treten sie durch die Basalmembran (wovon später die Rede sein wird), drängen sich zwischen die Zellen der Oberhaut," etc. Thus according to Loman the parent cells form a part of the hypodermis, and only differ from the conditions found in Polyclads in that their epidermal position is a secondary one. Loman presents no evidence, and in the face of the facts here presented his position is untenable.

Rhabditi are being constantly discharged from the epidermis during the life of the individual, and provision must be made for their renewal. Parent cells are therefore being continually produced to supply the steady demand of the epidermis for rhabditi. The evidence of this lies in the fact that in individuals of all ages these cells are found in all stages of development. Iijima ('84, p. 373) says "es sicher scheint, dass die Rhabditen nicht ausgestossen werden." If the rods are not dis-

charged from the hypodermis, why are they being continually developed throughout the lifetime of the individual? Something must become of them, or there would be an accumulation too great to find room in the hypodermis.

Kennel ('88, p. 474) says, relative to this subject: "Lässt man sie [planarians] aber in Uhrschälchen mit Wasser längere Zeit unbehelligt, so dass sie sich festsetzen, und stört sie dann plötzlich, so ziehen sie sich stark zusammen, machen heftige Bewegungen und suchen zu entfliehen. An der betr. Stelle aber findet man bei schneller Untersuchung Massen von Rhabditen in allen Stadien der Auflösung, und wenn man das Wasser schnell ausgiesst, findet man dort ein Klümpchen zähen Schleim, — die Stäbchen lösen sich in Schleim auf." I have often repeated the experiment of Kennel, and have always found rhabditi in large numbers in the slime secreted by the worm when placed on a glass plate.

We may now consider the question of the morphological and physiological meaning of the rhabditi. Two interpretations of the morphological value of the dermal rods have been given by naturalists. The larger number of observers consider them homologous with the nematocysts[1] of Cœlenterates; whereas the more recent investigators believe them to be the morphological equivalents of gland secretions. I coincide with the latter explanation, and offer the following arguments in its support. The parent cells are unicellular glands, and the rhabditi, their secretions, like the secretions of other dermal glands, are voided from the body of the individual. The rods cannot function as organs of touch in lending resistance to the epidermis, as suggested by Max Schultze and maintained by many others, for they do not lie in the epidermis cells, but between them. The insensible gradations that exist between rhabditi and the secretions of glands, as exemplified in the so called "Pseudorhabditen," "Schleimstäbchen," "Schleimblöckchen," and "Körnerdrüsen," have been to me one of the most striking evidences of the glandular significance of the rhabditi. The dermal rods of Phagocata, when acted on by reagents, present conditions resembling all the varieties of dermal bodies figured by Lang, and, as I have said elsewhere, I believe that the epidermal "gland-cells" of Moseley were only rhabditi modified by acids. Sub-hypodermal glands and the mother cells of the rods never occur together. Where rhabditi are absent, their place is taken by glands, and *vice versa*. This is illustrated in the region of the

[1] According to Camillo Schneider ('90, p 375) even the nematocysts are to be considered only as highly specialized secretory cells derived from simple gland cells.

gonopore and at the edges of the body. Another proof consists in the fact that the reaction with stains is always the same for both glands and rhabditi. With picrocarmine the effect is most striking. All the tissues of the body take the carmine except the rhabditi and the glands, both of which, owing to their yellow color, stand out in contrast to the rest of the body.

Keferstein ('68, p. 15) was the first to speak of the rhabditi as glandular secretions, and he called the parent cells "Stäbchendrüsen," and the rods "geformte Schleimmassen." More recently this view has been confirmed by Lang ('84, p. 52) and Kennel ('88, p. 474). The secretions both of the slime glands and of the accessory sexual glands often appear as rod-shaped bodies, and it was evidently this appearance of the secretions occurring around the sexual organs that led Jensen ('78, p. 11) to consider them rhabditi, and to speak of them as urticating organs functional during copulation, — the theory first suggested by Anton Schneider. Similar rod-shaped secretions are figured by Graff, who calls them "Schleimpröpfchen."

If we are to consider the parent cells as glands, what part do the rhabditi play in the economy of the worm? I must agree with Kennel, that the rhabditi are of use to the worm in securing food, and, I may add, serve also for protection. Phagocata, like all planarians, is carnivorous, and observation of its feeding habits has shown me that rhabditi are cast out of the body in large numbers, and that this condensed secretion helps to entangle and disable the prey. If one of the worms be placed on a glass plate with a very little water, it soon becomes hopelessly entangled in its own secretions, and when in this condition placed in abundant water, some minutes elapse before it can free itself and regain its activity. If some of the slime be examined with high powers of the microscope, it will be seen to contain many rhabditi, in all stages of dissolution. The rhabditi dissolve slowly in water, and it is by reason of this slow disintegration that the slime retains a thickness and tenacity that impedes the movements of an organism in contact with it long enough for the worm to lay hold of it with its many pharynges.

The conditions found in parasitic Turbellarians may be mentioned as evidence that this is the function of the rhabditi. Only four parasitic species have been studied histologically, three of which belong to the Rhabdocœles and one to the Triclads. In all of these forms rhabditi are absent, but in their stead are found sub-hypodermal glands which resemble the parent cells of rhabditi, and like them open to the exterior, — another illustration of the complementary occurrence of rhabditi and glands.

Von Ihering ('80, p. 149) states that in the case of Graffilla muricicola, from the kidneys of Murex, concretions and rhabditi are altogether wanting in the epidermis. Their function, he says, is one of protection, and hence they are not needed in a parasite. Lang ('80, p. 108) says of Graffilla tethydicola, from the foot of Tethys, that there are no rhabditi, but "Unmittelbar unter den Haut liegt eine grosse Anzahl eizelliger, birnförmiger, sich hauptsächlich mit Picrocarmine intensiv färbender Drüsen." Graff ('82, p. 375) says, concerning the same species, "Ueberdies finden sich hier unter der Haut zahlreiche einzellige birnförmige Drüsen." Anoplodium parasitica, a parasite in the body cavity of Holothuria tubulosa, also possesses no rhabditi: "Ich habe weder an frischen noch an conservirten Exemplaren von *stäbchenformigen* Körpern oder von irgend einem Pigmente etwas wahrnehmen können." (Graff, '82, p. 376.)

In Planaria limuli, a Triclad ectoparasitic on Limulus polyphemus, I have been unable to find any trace of rhabditi, but have found in abundance sub-hypodermal glands that resemble the parent cells of rhabditi, and like them send long ducts to the epidermis. Graff ('79, p. 203) states regarding this species that there are no true rhabditi; but he speaks of certain "Haftorgane," which he compares to rosettes of rod-like bodies, and then adds: "Die dieselben zusammensetzenden Stäbchen (Haftstäbchen) bilden sich im Innern des Körpers in besonderen Drüsen und färben sich äusserst intensiv in Carmine und Hämatoxylin," — but I could not find these organs.

Thus we see that in parasitic Turbellarians there are no rhabditi, their place being taken by many sub-hypodermal glands. Assuming that the rhabditi are condensed secretions used in securing prey and for protection, the conditions present in parasitic forms are in every way consistent with our conclusions. The only other possible function for the rhabditi is that assumed by Graff ('82, p. 58) and stated by him as follows: "Die plausibelste Anschauung ist auch heute noch die von Schultze gegebene und von Stein auch für die Stäbchen der Infusorien adoptirte, wonach die Stäbchen indem sie dem äussern Drucke einen Widerstand entgegensetzen, in ähnlicher Weise befördernd auf der feinere Tastgefühl der Haut einwirken, wie der Nagel auf Tastvermögen der Fingerspitze." I have shown that on account of their intercellular position the rods probably cannot have such a function; but even if this evidence were considered insufficient to disprove their supposed office, one would have to encounter the objection that so important a function would not be likely to be entirely lost in parasites, particularly in such active ectoparasites as P. limuli, where the parasitism is of

such a nature that sensory organs would still be of great importance in the animal's economy.

To summarize, then, *the dermal rods are to be considered as condensed secretions arising in sub-hypodermal unicellular glands of ectodermic origin. All gradations exist between rhabditi and the secretions of normal glands. The rhabditi are being continually cast out of the body, and replaced by new ones developed in new parent cells within the body parenchyma. The connection of the parent cells with the epidermis is a primitive one, and the rods pass to the exterior by means of the tubular ducts formed by the neck of the elongated cells. The rods lie between the cells of the epidermis; they are slowly soluble in water, and are used by the animal in securing food and for protection.*

The *basement membrane* is a homogeneous layer immediately under the hypodermis, the cells of which are directly connected with it. It varies in thickness in different individuals and in different parts of the same individual; 1 μ and 6.5 μ are the extremes that I have found. It stains deeply in all of the carmine dyes, and always takes a darker color than the underlying muscles. A granular condition, such as is mentioned by Iijima ('84, p. 375), does not exist, nor is there any appearance of the fibrous structure described by Lang ('84, p. 63) for Polyclads. Minot ('77, p. 408) states that the basement membrane is composed of circular fibres. The only appearance in Phagocata approaching that described by Minot is seen in surface views of bits of the membrane occurring in isolation preparations, where on one surface there appear parallel markings; but these are no doubt due to the intimate contact of the membrane with the circular muscle fibres. The membrane is closely applied to the muscle fibres, and in longitudinal sections, where the circular muscles are cut across, the inner contour appears uneven, owing to the projecting ridges which it sends into the intermuscular spaces (Figs. 4, 6, 7, and 10); stated in another way, the circular muscles may be said to indent the basement membrane, leaving their impression in the form of parallel grooves on its under surface. In cross sections of the worm, the inner border of the membrane appears perfectly smooth, and parallel to the circular muscles (Fig. 2). The only departure from homogeneity is caused by the fine channels occupied by the processes of the parent cells of the rhabditi (Figs. 1, 4, 6, 7, and 10), and these are only transitory, soon becoming obliterated. Occasionally pigment granules find their way through these openings, and may become caught in the basement membrane.

There can be little doubt that the basement membrane is a product of the hypodermis. There is a direct relation between its thickness and that of the latter; hence it is thickest on the dorsal, and thinnest on the ventral surface of the animal. It is true that the hypodermis is easily separated from the membrane, but on the other hand the intimate relation between the two structures is evident from the manner in which the cells of the former remain attached to the latter after the rhabditi have been removed by partial maceration (Fig. 3); and even when the hypodermis has been entirely removed, the outer contour of the membrane in regions where, in consequence of the presence of many rhabditi, the hypodermal cells have become much compressed, appears irregular, the uneven projections representing the points of attachment of the hypodermal cells. In those regions where the rhabditi are few or absent, the basement membrane presents a comparatively smooth surface. There is no evidence in Phagocata that the membrane is an independent cellular tissue, as in Polyclads, since no traces of structure could be demonstrated, the membrane appearing homogeneous with all of the stains that were employed. In my opinion, therefore, the basement membrane is of hypodermal origin.

The *pigment* in Phagocata occurs in the form of fine granules, of an irregular outline and of a dirty greenish color. It lies principally in the longitudinal bands of muscles between the fibres, so that, when a worm is put under pressure and viewed with moderate powers, the pigment appears as if arranged in parallel rows running lengthwise of the animal. In the deeper tissues, below the muscle bands, the pigment occurs in patches and streaks (Fig. 1). No pigment occurs normally in the hypodermis. There are no special pigment cells; the pigment occurs in the form of distinct separate granules, which are intercellular in position, never intracellular. The origin of pigment as isolated granules might be explained by some such theory as that of Eisig ('87, p. 765), by which it is to be considered as a product of the excretory system, — a kind of utilized excreta.

There are only three systems of *muscles:* the circular, the longitudinal, and the sagittal or dorso-ventral. As compared with the complicated musculature of other fresh-water planarians, that of Phagocata is much simplified, and in this respect it agrees with Gunda sementata (Lang, '81[a], p. 193) and Planaria abscissa (Iijima, '87, p. 344). The circular muscles form a single layer immediately under the basement membrane, to which, as we have seen, they are closely applied. The longitudinal muscles form a thick band inside of the circular layer, and are much

thicker on the ventral side (Fig. 10) than on the dorsal (Fig. 1). In cross sections the longitudinal muscles appear separated into bundles, between which the ends of the dorso-ventral fibres are seen passing to the basement membrane, into which they are inserted. I have not been able to find a nucleus in or on either the circular or longitudinal muscle fibres. The nucleus of the dorso-ventral fibres is eccentric, as in the muscles of Planaria torva, figured by Ratzel ('69, p. 275, Taf. XXIII. Fig. 26). In cross sections both circular and longitudinal fibres have an irregular outline and show a differentiation into an outer highly refractive contractile portion and an inner feebly refractive axis (Plate I.). Branching ends were observed only in the sagittal fibres.

A reticulate *mesenchyma* constitutes the greater portion of the substance of the body, occupying all the spaces between the organs. The spaces left by the irregular network formed by the branching cells (Plate II. Fig. 18) are connected with one another, and are to be considered as a kind of pseudocœle; they are filled with a granular perivisceral fluid. The sagittal muscle fibres in some places appear to be directly continuous with branches of the mesenchyma cells (Plate II. Fig. 18, *mu. sag.*), so that by contraction of the muscles the sizes of the spaces would be altered, and thereby the perivisceral fluid would be set in motion, thus establishing an irregular circulation in the pseudocœle. Lang ('84, p. 83) maintains that in the case of Polyclads these spaces are intracellular in their origin, and that the so called perivisceral fluid is the result of a liquefaction of the plasma of the connective-tissue cells, which thus become vesicular, and finally, by the breaking through of their thin walls, form a network. But if the pseudocœlar spaces were intracellular in their origin, as claimed by Lang, it would be more difficult to understand the intimate relation between the muscles and the processes of the reticulated parenchyma cells; it would not, however, be in any way an exceptional condition for muscle fibres to be attached to the prolongations of *stellate* connective-tissue cells, more especially when we consider that the muscle fibres and mesenchyma cells have a common origin. As is well known, the Hertwigs have produced evidence to show that the mesenchymatous muscles of the Pseudocœlous animals are "besonders differenzirte Zellen der Bindesubstanz" ('81, p. 98). Moreover, the mode of origin maintained by Lang is not founded, as far as I understand it, on evidences from embryonic conditions. Graff ('82, p. 72) was unable, from the evidence found in Rhabdocœles, to establish "a distinction between muscle fibres and connective-tissue fibres"; and Hamann ('85, p. 96) has shown that in Echinoderms the connective-

tissue cells are in direct continuation with the muscle fibres of mesenchymatous origin. From the study that I have made of the conditions in Phagocata I am convinced that they are like those found in Rhabdocœles.

Imbedded in the mesenchyma are the parent cells of the rhabditi and also the glands that open at the surface in different regions. There are two large accumulations of glands that open to the exterior, one around the gonopore, the other on the ventral surface of the head region. A smaller accumulation exists near the posterior end of the body. The glands that occur in the head region afford important evidence of the morphological equivalence of rhabditi-producing cells and ordinary dermal glands. The deep ends of these glands are located behind the brain, between it and the ovaries, and in passing over the brain they run downward and forward till they open out on the ventral surface of the head close to its anterior margin. They are numerous, and occur in two bundles or groups, one on either side of the median plane of the body. They appear as long sinuous tubes with enlargements or swellings occurring at intervals (Plate II. Fig. 17), but without any evidence of branching, and it has not been possible to distinguish between the gland proper and its duct. Not being uniformly distributed, the finely granular contents of the tubes cause the irregular enlargements referred to. Nuclei could not be detected in any portions of the ducts. The two bundles of glands begin immediately in front of the ovaries, and as they pass forward converge, so that when they pass over the commissure of the brain they are in contact with each other; but they soon diverge again, and make their way to the surface as already described. These two bundles of glands I believe to be the homologues of the "Stäbchenstrassen" found in Rhabdocœles, and most prominently in the Mesostomidæ. Both the position and the course of the glands in Phagocata are identical with those of the "Stäbchenstrassen" in Rhabdocœles, and the "wiederholte Anschwellungen" (A. Schneider, '73, p. 83) in the latter correspond to the repeated enlargements in the former. The glandular organs of Rhabdocœles differ from them only in the nature of their contents. Furthermore, the almost complete absence of rhabditi in the head region of Phagocata strengthens this conclusion. One has only to compare Leuckart's ('52, p. 23) description of Mesostomum and the figures given in Graff's great monograph with the conditions present in Phagocata, at once to recognize the probable equivalence of these structures. A similar but smaller accumulation of glands is found at the posterior extremity of the body in Phagocata, and it is worthy of note that there is likewise in Rhabdocœles an accumulation

of rhabditi-secreting organs in the same region. The slime-secreting glands at the extremities of the body are used in Phagocata as a means of attachment, for it is principally by its extremities that the worm fastens itself to objects, as can be seen when one attempts to remove it from the side of the aquarium.

The other glands that are imbedded in the mesenchyma are those which open around the genital orifice. Together with their ducts they resemble in form the parent cells of the rhabditi; they also react like the glands of the head region with all stains. A portion of one of these glands from an isolation preparation is represented in Plate IV. Figure 41.

The *digestive apparatus* of Phagocata is like that of other Triclads, except in regard to the number and arrangement of the pharynges, which form such a striking feature of this species. The form, position, relations, etc. of these pharynges have already (p. 4) been described, and it has also been stated that at the junction of the three main tracts of the intestine there is one pharynx which is larger and more prominent than the rest (Plate II. Fig. 20, *phy. m.*), and that this is the homologue of the single pharynx of other Triclads. There is no difference in histological structure between this median pharynx and those which connect with the lateral tracts. In a cross section of a pharynx (Plate II. Fig. 12) the following layers can be distinguished, beginning from the outside: (1) the fine cilia covering the external surface, (2) the external epithelium, (3) a single layer of longitudinal muscle fibres, (4) a single layer of circular muscles, (5) a wide zone occupied by connective-tissue cells and salivary ducts and traversed by radial muscle fibres, (6) a single layer of longitudinal muscle fibres, (7) a broad band of circular muscle fibres, (8) the internal epithelium, and (9) the cilia lining the lumen (compare also the longitudinal section shown in Fig. 16). The external covering of cilia disappears at a region about two thirds of the distance from the free end of the pharynx toward its insertion on the intestine, and the epithelium there loses its smooth appearance, becoming wrinkled and creased. The cilia that line the lumen of the pharynx are more restricted in their distribution, and are lost at about one third of the way from the extremity, where the internal epithelium also becomes longitudinally folded, many of the folds projecting far into the lumen of the pharynx (Plate II. Fig. 12, *e'th. i.*). In this portion of the epithelium there are many nuclei, whereas in the ciliated region nuclei cannot be seen. Compare Figures 12 and 16, Figure 12 being a cross section which passes through the non-ciliated portion of

the internal epithelium. There are no nuclei anywhere in the external epithelium of the fully developed pharynx, except near its proximal end. By the use of silver nitrate, however, I have been able to demonstrate that the layer is a true epithelium. Isolated pharynges were killed with hot 1% silver nitrate. By using the solution hot, the pharynges were killed in an extended condition. A tangential section through material treated in this way is represented on Plate IV. Fig. 47. I have been unable by any method of staining to demonstrate the presence of nuclei in these cells, the boundaries of which are so plainly brought out by impregnation with silver.

In young pharynges (Plate II. Fig. 14), where the tissues are not fully differentiated, nuclei are to be seen in both the external and internal epithelial coverings, although no trace of them can be found later on. It is not difficult to find pharynges in different stages of development, since the number increases with the age of the individual. The young pharynx begins as a solid bud of tissue projecting into a cavity hollowed out of the mesenchyma. The cavity is lined with a layer of flattened cells, which is continuous with the cell layer covering the young pharynx (Plate II. Fig. 11). The cavity is at first closed on all sides, but eventually communicates with the common pharyngeal chamber. The lumen of the pharynx is formed by an infolding of its free end, which projects into the cavity. Although I have not been able to trace directly all the steps in the invagination, I have seen specimens where the lumen was lined throughout with an epithelium, and where there was as yet no connection with the intestine. The epithelium lining the lumen is continuous with that covering the outer surface of the young pharynx, and hence with that lining the pharyngeal cavity, and it presents the same histological conditions as the latter (Plate II. Fig. 11). Figure 14 represents a cross section of a young pharynx somewhat advanced in development, where the cellular structure of both the inner and outer epithelium is still evident; there are as yet no cilia, and no traces of the longitudinal muscles. I expect to describe in another paper the changes by which the mass of indifferent cells composing the young pharynx is converted into the ultimate histological structures of the mature pharynx.

The outer layer of the pharynx has never been described as possessing a distinctly cellular structure. Moseley ('74, p. 131), in speaking of land planarians, describes "an epithelium in which no definite cell structures could be observed; but it appeared transparent, and marked by vertical lines which might represent separation into cellular ele-

ments." Iijima ('84, p. 389) also saw "eine senkrechte Streifung." Lang ('81, p. 196, and '84, p. 109) speaks of it as a "cuticulaänliches Epithel" with flattened nuclei which it was difficult to see, and Minot ('77, p. 426) gives to it a well defined basement membrane. It is obvious from the description that I have given of the young pharynx that the outer layer, though ultimately much modified in appearance, is nevertheless an epithelial layer.

I could not demonstrate the presence of a cuticula with pore canals such as has been described by Iijima ('84, p. 390); neither could I discover anything answering to the nerve plexus described for other forms, nor could I detect any nerve tissue. From the automatic movements of the isolated pharynges, one would expect to find a complicated system of nerves, and perhaps one or more ganglionic centres.

In the mature pharynges the radial muscle fibres run from the outer to the inner epithelium, to both of which they are attached by their finely branched ends (Figs. 12 and 16). These muscles no doubt act antagonistically to the broad band of circular muscles in dilating the lumen of the pharynx, and by means of these two systems the peristaltic motions displayed by the pharynges are accomplished. Between the radial fibres there is a network of connective-tissue cells, and in the outer half of this middle zone occur the salivary ducts (Figs. 12 and 16, *dt. sal.*), which run the whole length of the pharynx and open at the edge of its lip. In the meshes of the connective-tissue network are seen fine granulations; these spaces are undoubtedly in communication with the pseudocœle of the body mesenchyma, and it is to the coagulation of the perivisceral fluid which has made its way out into the tissues of the pharynges that is due the granular appearance seen.

I have little to add to what has been written concerning the histology of the intestine, my observations agreeing in the main with those of Iijima. The structure is the same in the principal tracts and in the smaller branches; there are no differentiated gland cells. During the periods of most active digestion the intestinal cells are filled with highly refractive oil-like globules, of different sizes (Plate IV. Fig. 43), — the food matter absorbed by the cells. In this condition the cells are large, and protrude into the lumen, so that in the smaller branches of the intestine the latter has entirely disappeared. The contents of the cells are eventually absorbed by the neighboring tissues, and the intestinal cells themselves then appear vacuolated.

I have not been able to trace out the course of the *excretory canals*. Although I have endeavored many times to study them, I have never

seen more than a few loops in the head region, and these were seen only when the animal was put under great pressure, resulting in disintegration of the tissues.

The *nervous system* of Phagocata agrees in the main with the descriptions given by Lang ('81, p. 53) and Iijima ('87, p. 349) for other planarians. The longitudinal nerve trunks unite near the anterior end of the body in a well developed brain mass (Plate III. Figs. 25 and 33), and posteriorly are connected with one another by fine commissures. Larger commissures unite the trunks to one another throughout their whole length, either running straight from trunk to trunk, or branching in their passage (Plate IV. Fig. 38). The latter condition may be regarded as closely related to one in which two commissures are united to each other by means of a connective, a condition that often occurs. There is no fixed relation between the number of transverse commissures and the lateral diverticulæ of the intestine, but lateral nerves are usually given off from the main stems at points opposite to the union of the latter with transverse commissures (Plate IV. Fig. 38). The main nerve trunks are prolonged anterior to the brain. They diminish rapidly in size, and give off several lateral branches, which are directed obliquely forwards and outwards (Plate III. Figs. 25 and 36), and they finally break up into minute branches which form a network. The lateral nerves from the main trunks run, sometimes with, sometimes without branching, to the margins, where they unite with a second pair of finer longitudinal nerves, — the marginal or peripheral nerves (Plate IV. Fig. 37, *n. pi'ph.*). The marginal nerves form the lateral edges of a great nervous network, which lies near the ventral surface just inside the sheet of longitudinal muscles. Figures 37 and 38 represent portions of two successive horizontal sections close to the ventral surface. The sections are 30 μ thick, and pass through the floor of the pharyngeal chamber; the light areas show where the knife has cut through the wall into the pharyngeal cavity. The animal having been sectioned from the ventral side, Figure 38 is the deeper (i. e. more dorsal) section. The position of the oral opening (*o*) indicates that the portions of the sections shown are from the same region of the body. In Figure 38 are seen the main nerve trunks (*n. l'p.*) together with transverse commissures (*com. t.*) and lateral nerves (*n. l.*). It may be seen from Figure 37 how the median branches from the peripheral nerves (*n. pi'ph.*) break up into a network or plexus, which is distributed to the muscles (*plx. mu.*). This network covers the whole of the ventral surface, and at the extreme anterior end of the body is continuous with finer ramifications of the

anterior longitudinal trunks. I could find no trace of a similar plexus in connection with the less developed muscles of the dorsal side.

The nervous system of planarians may be readily understood, it seems to me, if we regard it as composed of two more or less distinct parts, — a deep-seated and a more superficial portion. The deep-seated and more central part is present in all planarians hitherto investigated, and consists of the brain, longitudinal nerve trunks, their commissures, and the lateral nerves given off from them. The superficial portion consists of a nerve plexus which lies just underneath the longitudinal muscles, and may be confined to one or the other of the two surfaces, or may be wholly wanting. A conspicuous part of this superficial system, whenever it exists, is the marginal nerve. The connection between the deep and superficial portions of the nervous system is effected by means of vertical nerves running between the two, and, as I have found in Phagocata, the marginal nerve also serves in an indirect way the same purpose; for on the one hand it is connected with the lateral nerves of the central system, and on the other it forms the marginal terminus of the superficial system.

Lang ('81, p. 72) has described in Gunda a marginal nerve directly connected with the lateral nerves given off from the main trunks, but has been unable to find any other evidence of a plexus. In Rhynchodesmus, according to the same author ('81, p. 62), there are both dorsal and ventral plexuses, which are in contact with the deep surfaces of the longitudinal muscles, and are connected with the central system by vertical branches from the main trunks, from the lateral nerves, and from the transverse commissures, but there is no peripheral nerve. Lang ('81, p. 57) also finds a plexus in connection with the deeper longitudinal muscles in Planaria torva. Iijima ('84, p. 426) has likewise found a dorsal plexus in a similar position in Pl. polychroa and in D. lacteum, and Loman ('87, p. 76) has found the same conditions in Bipalium sumatrense and B. javanum. In Gunda ulvæ and Pl. abscissa there exists, according to Iijima ('87, p. 349), a second, dorsal pair of longitudinal stems, giving off branches that break up into a plexus and unite with the plexus from the lateral branches of the main trunks, the whole forming a "Nervenschlauch." He says that a "Randnerv" is present, but he does not state what are its relations to the plexuses.

From this brief survey it is obvious that Gunda represents one extreme, and Rhynchodesmus the other; since in the former there are no superficial plexuses, and in the latter there is a superficial plexus on both dorsal and ventral surfaces in addition to the parts found in Gunda,

except that Rhynchodesmus has no marginal nerve. Both Phagocata and Planaria abscissa are intermediate between these extremes, Pl. abscissa possessing only the dorsal portion of the superficial system (in which a special dorsal longitudinal nerve has arisen), and Phagocata having only the ventral portion of that system. Both possess, however, the marginal nerve found in Gunda, and I believe that it probably sustains in Pl. abscissa the same relations to the deep portion of the nervous system that I have found to exist in Phagocata.

It is evident, I think, from what I have shown in Phagocata, that the marginal nerve is to be regarded as one of the means of communication between the central and superficial parts of the nervous system; or perhaps rather as a differentiation of that portion of the superficial system which is put in connection with the deep system by means of the lateral branches from the main trunks.

It may perhaps be reasonable to suppose that the more concentrated condition in Gunda has been brought about by a process of centralization from the more diffuse and more primitive (?) condition shown in Rhynchodesmus.

The brain is formed on the same plan as that of Gunda (Lang, '81, p. 67; '81[a], p. 213). I find two commissures, a larger anterior commissure which Lang calls in Gunda the sensory, and a smaller posterior one which he calls motor (Plate III. Figs. 23, 33, and Plate IV. Figs. 39, 46). The posterior commissure lies somewhat behind and below the anterior one. It directly connects the longitudinal nerve trunks, since it lies in the same ventral plane with them, while the anterior commissure, occupying a higher plane, is only indirectly united to these; viz. by means of the lateral masses of the brain from which vertical commissural fibres (the motor-sensory commissures of Lang) extend to the nerve trunks. Lang describes four pairs of nerves as arising from the lateral sensory masses of the brain. I cannot discover that there is any fixed number in Phagocata. The only well defined one is the optic nerve (Plate IV. Fig. 40, *n. opt.*). A great sheet of fine nerves is given off from the lateral surface of the brain, and, spreading out fan-like, runs forward to the anterior margin of the body (Plate III. Figs. 25 and 34, *n.*). It is from these nerves that the "Tastorgane" of this highly sensitive portion of the body receive their nerve supply.

A comparison of the figures will make clear the relation of the different parts of the brain. Figures 26 to 31 are from cross sections through the region of the brain taken at intervals of 60 μ. Figures 32 to 36 are consecutive sections in the horizontal plane, Figure 32 being the most dorsal of the series.

Lang ('81, p. 79) speaks of a "Zellenbeleg von wirklichen Ganglienzellen" around the brain of Triclads. Iijima ('87, p. 353) describes these cells as being unipolar with extremely delicate processes. I also find a layer of closely packed cells with large nuclei around the brain, more especially about the so called sensory portions (Plate III. Figs. 26–31, Plate IV. Figs. 39 and 40), but I cannot say that these are ganglionic cells. They resemble in every way connective-tissue cells; they react like them with stains, and are more prominent only on account of their compact arrangement. The nuclei of the two large "Substanzinseln" in the lateral masses of the brain (Plate III. Figs. 28, 33, Plate IV. Fig. 39, *con't. tis.*) are both identical and continuous with the nuclei surrounding the brain, and those found in the main nerve trunks cannot be distinguished from them. The ganglionic cells occurring *in* the nerve tissue are not as large, nor do their nuclei stain as deeply, as those occurring *around* the brain mass. I therefore believe that the latter belong to the mesenchyma, and that the "Substanzinseln" are only intrusive connective tissue.[1] Aside from this, I can add nothing to the observations of Iijima on the finer structure of the nervous tissue. The longitudinal nerve trunks in some places appear to be double for a considerable distance, being split, as it were, by the ingrowth of mesenchymatous tissue (Plate III. Figs. 33 to 36, and Plate IV. Fig. 38). All such openings, as pointed out by Lang ('81, p. 56), occur between the points of origin of the lateral nerves.

The *testes* are numerous, and are found lying close together throughout the whole length of the animal. Their development takes place before that of the yolk glands. While the latter are still in an early stage of development, spermatogenesis has been completed, the testes have disappeared, and the spermatozoa are found filling the vasa deferentia. The testes first appear as spherical clusters of cells, which by division increase in number and arrange themselves in the form of hollow spheres. Some of the peripheral cells divide rapidly into small spherical cells, that come to lie in the cavity of the testis. These cells become elongated or pear-shaped, and are then differentiated into two portions, a deeply stainable thickened end, and a tapering tail portion (Plate II. Fig. 24). Further elongation takes place, until the form

[1] Since I came to these conclusions in regard to the mesenchymatous character of the so called "Substanzinseln," I have been gratified to learn that my conclusions agree with those of Lonian ('87, p. 77). In Bipalium, then, as well as in Phagocata, the "Substanzinseln" present in all particulars the same differences from ganglionic cells.

of the adult spermatozoön is reached. Many stages of development can be seen in the same testis. The different stages occur in distinct groups, each group probably being the product of one of the parent cells. The wall of the testis, when the spermatozoa first begin to develop, is composed of many cells, most of which by division go to form spermatozoa; a few of the cells, however, are differentiated into flattened epithelium, which constitutes the wall of the capsular testis (Plate II. Fig. 24, *e'th.*).

I have not succeeded in ascertaining the exact manner in which the spermatozoa find their way into the vasa deferentia, but Iijima's statement ('84, p. 408) that they do not wander through the spaces of the mesenchyma is certainly incorrect. The testes give rise to tubular prolongations, but whether these are directly connected with the vas deferens or first unite into one or more vasa efferentia, I cannot say. The testicular canals appear to be direct outgrowths of the wall of the testis. Their walls and those of the vasa deferentia have the same simple structure (compare Plate II. Figs. 23 and 24), being composed of a single layer of thin epithelium. The nuclei in the walls of the tubes often occur in pairs, and thus suggest that the cells to which they belong have recently undergone division (Fig. 24).

According to Moseley ('74, p. 139), the testes in land planarians open directly into the vasa deferentia; Minot ('77, p. 432), on the contrary, speaks of fine testicular canals that unite to form larger tubes. Kennel ('79, p. 137) states that the testes, arranged in rows, fuse to form the vasa deferentia.

The anterior ends of the vasa deferentia in Phagocata lie on either side of the pharyngeal chamber in the region of the mouth opening. They have the form of large elongated sacs (Plate IV. Fig. 42, *x*) which open into comparatively narrow tubes (*va. df.*), which are of an even calibre, and much convoluted and twisted. They run backward parallel to each other until near the base of the penis; they then turn at right angles toward the middle plane, where they unite to form a single tube which terminates at the apex of the penis. The spermatozoa when ripe leave the testes by the testicular canals previously described, and pass into the vasa deferentia, which become filled from their enlarged blind ends up to a point beyond that where they unite to enter the penis. Here the spermatozoa remain stored until arranged into spermatophores, in which form they pass into the vagina of another individual. After the spermatozoa have found their way to the vasa deferentia, all traces of the testes disappear.

Physiologically considered, the vasa deferentia of Triclads are to be

considered as vesiculæ seminales. In Polyclads and in Rhabdocœles a vesicula seminalis is present. This organ has been described for land planarians by Moseley ('77, p. 278) and Loman ('87, p. 81), and Kennel ('88, p. 460) speaks of "mehrfach gewundenen Samenblasen" in Planaria alpina. There can be no doubt that the terminal enlargements found in Phagocata are a provision for the storage of a great number of spermatozoa, as their size is found to vary in different individuals and on different sides of the same individual according as the number of spermatozoa is large or small.

The *penis* or intromittent organ is a highly muscular plug-like structure (Plate IV. Fig. 42, *pe.*) that lies in the genital atrium or penis sheath. It is covered with a flattened epithelium, under which there are alternating layers of circular and longitudinal muscles, five of each, forming a thick zone. Immediately outside the epithelial lining of the tube there is a band of circular muscles, and between these and the outer muscles there is a broad zone occupied by a meshwork of muscular fibres, prominent among which are those having a radial direction. The lumen of the penis is not of an even calibre, but consists of a succession of chambers, or dilatations, lined with a granular epithelium, which is probably glandular. It is within the lumen of the penis, no doubt, that the spermatophores are formed. The sheath of the penis is lined with an epithelium of cylindrical cells, the nuclei of which lie close to the bases of the cells, and are stained deeply, while the glandular cell substance is stained only slightly. These cells also may be glandular, but if so, I can find no explanation for their faint reaction with staining reagents. In that respect they differ from all other glandular tissue.

The female sexual organs consist of a pair of ovaries with their oviducts, the vitellarium or yolk gland, the uterus, and the vagina. The single pair of *ovaries* is situated in the anterior part of the body a little behind the brain mass. They are symmetrically placed on the ventral side of the body just dorsad of the main nerve trunks, one on either side. They appear as rounded sacs filled with ova (Plate II. Fig. 21). The wall of the ovary is a delicate membrane, in which I could detect no sign of cell structure, such as Moseley ('74, p. 137) found in the ovary of land planarians. Scattered in between the ova are the nuclei of a connective-tissue network that fills the spaces between the ova (Plate II. Fig. 21, *nl. con't. tis.*). Iijima ('84, p. 412) considers the branching cells between the ova as rudimentary egg cells, at whose expense the ova develop. I have not yet seen different stages in the development of the ova.

Intimately associated with the ovaries are two prominent compact cell masses with deeply stained nuclei, which may provisionally be called *parovaria* (Plate II. Fig. 21, *vt'm.*). They are larger than the ovaries, and envelop them above, in front, and on the outside; that is to say, the ovaries are surrounded on three sides, being partially imbedded, so to speak, in these cell masses. The latter are present in every individual, and their size relative to that of the ovaries varies only with the condition of the sexual organs. They are smallest during the development of the spermatozoa, and are most prominent at the time when the yolk glands have reached their full development. For a long time these cell masses puzzled me. I believed them to correspond to the second pair of rudimentary ovaries described by Iijima ('84, p. 412) for Polycelis tenuis, and I at first accepted his interpretation of their significance; but sections through additional material, where the female organs were not so advanced, served to show their true meaning; *they are the organs which give rise to the yolk glands.* At an early stage in the development of the testes no yolk glands are present, but they begin to appear at the time when the spermatozoa are ripening.

The first traces of the *yolk glands* are seen in branching chains of cells, which arise as outgrowths from the parovaria. Each cell has a large nucleus that is stained deeply in carmine. In these chains the cells lie either in a single row, or it may be in several rows (Plate II. Figs. 19 and 19*a*). The nuclei are large and granular, and occupy the greater part of the cell. It is to be inferred that the cells are dividing rapidly, since nuclei are found in all stages of division, and two nuclei are frequently seen in the same cell; the division appears to be direct, or amitotic (Plate II. Figs. 19 and 22). The rudimentary yolk glands occupy at first the ventral regions around the oviducts, but afterwards they send branches from there dorsad, until there is formed a dendritic system of rapidly dividing cells, which ramify through the tissues. From each of the cell masses around the ovaries is derived one half of the yolk system, that belonging to its own side of the body. The cell chains of the young yolk glands are seen to be directly connected with the parovarial cell masses, and histologically the structure of the two is identical (compare Fig. 19 with Fig. 22, Plate II.). Furthermore, at the time of development of the yolk glands there is a very active division of the cells of the parovarial masses, a condition that does not exist when the yolk glands have matured. A similarity in the condition of the cells of the yolk glands and those of the parovarial masses is evident at all stages of development. The young cells of the yolk

glands increase in size, but do not grow as rapidly as the surrounding protoplasm, and therefore the nucleus becomes smaller in proportion to the size of the cells. Many highly refractive granules appear in the protoplasm, and increase in number with the growth of the cells, till eventually, when the cells have attained their full size, they form a relatively large proportion of the cell mass (Plate IV. Fig. 45). Corresponding to the changes that take place in the yolk cells, there is a slight increase in the size of the parovarial cells, in which there is also an accumulation of highly refractive granules (Plate IV. Fig. 44), but the nuclei retain more nearly their original proportions to the cells than in the case of the yolk cells. In addition to the identity of histological structure, a most striking evidence of the derivation of the yolk glands from the parovarial cell masses is found in the reaction of both kinds of cells with staining fluids, more especially with picrocarminate of lithium. Figures 44 and 45, Plate IV., represent respectively sections through parovarial cells and mature yolk-gland cells of the same individual. Figures 19 and 22, Plate II., are sections from another individual; Figure 22 is a section of young parovarial cells, and Figure 19 of incipient yolk-gland cells. Upon comparison of Figures 19 and 22 with Figures 45 and 44, it will be noticed that, in addition to the appearance of the granules in the protoplasm of the older cells, there has been an increase in the size both of the yolk cells and of the cells of the parovarium. It is my belief, then, that the two large dendritic yolk glands arise by cell proliferation from the parovarial organs which exist in intimate relation with the ovaries.

Iijima ('84, p. 412) describes a pair of structures lying in front of the ovaries in Polycelis tenuis as being composed of a solid mass of cells, and as resembling young ovaries, so that this species possesses, in his opinion, two pairs of ovaries, one of which is rudimentary. On account of their terminal position, he considers these rudimentary structures, although not the functional ovaries, as the homologues of the single pair of ovaries present in other species. His account of the growth of the yolk glands, as given at p. 417, coincides with my observations, but concerning the source of the chains of young yolk cells he says (p. 455): "Wir dürfen sagen, dass die Dotterstränge durch Vermehrung einzelner Zellen, welche in dem Mesenchym sich befinden, ihren Ursprung nehmen." But his evidence that the "Dotterstränge" arise *in situ* is not satisfactory. It is to be regretted that he has not given a fuller account of the so called rudimentary ovaries of Polycelis, which, I am almost certain, are the equivalents of the parovarial cell masses of Phagocata.

The absence of yolk glands in Moseley's land planarians can be accounted for by assuming that in his material they were not yet ripe, as was probably the case. He states ('74, p. 137), however, that there is occasionally present in Bipalium, "just externally to the lower extremities of the ovaries, a small mass of large nucleated cells connected by a pedicle with the ovary itself." He considers that "it may represent a yolk-gland in a rudimentary condition." With this I fully agree, and further believe that this rudimentary yolk gland is the homologue of the structure which in Phagocata I have called parovarium.

The presence of a vitellogenous organ in Phagocata, together with the condition found in Polycelis by Iijima and in Bipalium by Moseley, suggests a discussion of the relations of the ovaries and vitellaria. Yolk glands have long been considered as resulting from the differentiation of the ovaries. Gegenbaur, as stated in his text-book ('70, p. 281), considers the yolk glands to be "Theile eines ansehnliches Ovars." Hallez ('79, p. 63) maintains that "le *vitellogène* n'est autre chose qu'une partie différenciée de l'ovaire," and according to Lang ('81[a], p. 228), "Die Keimstöcke und Dotterstöcke der Tricladen sind einander gleichwerthig. Sie entstehen aus Zellen, die anfangs nicht von einander unterscheiden lassen." Among Rhabdocœles all gradations are found, from an undifferentiated "Keimdotterstock," where ova and yolk cells are developed in different portions of the same organ, to conditions in which the ova and yolk cells are produced in distinct and separate organs. The yolk glands, then, have arisen by a divison of labor from a simple germ gland, as has already been formulated by Graff ('82, p. 130) in the following words: "Die Keimdotterstöcke müssen wir uns aus Ovarien durch einfache Arbeitstheilung hervorgegángen denken; durch räumliche Trennung der verschieden functionirenden Abschnitte des Keimdotterstockes entstanden schlieslich die Keim- und Dotterstöcke." I consider the condition found in Phagocata to be less differentiated than that exhibited by Pl. tenuis (Iijima), inasmuch as the cells which form it still retain a more intimate relation to the true ovary than they do in the latter case.

The union of the yolk glands with the oviducts is a secondary one; it takes place at intervals throughout their length. I have not studied this in detail, but, as far as I have learned, the conditions agree with the careful description given by Iijima ('84, p. 415). The oviducts open into the vagina just above the point where it enters the genital atrium (Plate IV. Fig. 42).

The *uterus* (Plate IV. Fig. 42, *ut.*) is a sac-like organ lying just anterior to the penis, and has thick walls that are thrown into many

folds. It is lined with an epithelium of elongated cylindrical or pyriform cells of a glandular nature. The appearance of the cells varies with the activity of their secretion; the protoplasm may be either homogeneous, or filled with oil-like globules, or it may be vacuolated. The cells rest upon a fine basement membrane. There is no musculature, and there are no cilia.

The mouth of the uterus is prolonged into a tube with thick muscular walls, *the vagina* (Plate IV. Fig. 42, *vag.*), which runs backward, passing above and to the left of the penis and then dipping down toward the ventral side of the body, where it opens into the genital atrium. Where the vagina arises from the uterus it is lined with a ciliated epithelium of low cubical cells, and possesses a musculature of circular and longitudinal fibres. As it passes backward, the cells of the lining epithelium become taller and cylindrical (Plate II. Fig. 15, *e'th.*), and the nuclei are elongated. The outer ends of the cells show distinct granulations, and the contour of the lumen becomes uneven; the glandular nature of the cells now becomes apparent. Along with the change in the appearance of the cells of the lining epithelium there is an increase in the thickness of the musculature, which now consists of alternating layers of circular and longitudinal fibres. The musculature of the vagina reaches its greatest development at the point where it bends toward the ventral side of the body; from this point onward the cells lose their glandular character, and the musculature diminishes in thickness, till, at the point where the vagina receives the oviducts, it again consists of only a single layer each of circular and longitudinal fibres. Moseley ('74, p. 141) and Iijima ('84, p. 420) speak of radial fibres in the walls of the vagina; but I could not find any.

The accessory female organs of Triclads have been the subject of much discussion. There are no other structures about which so many opinions at variance with each other have been advanced. The organ which I have called the uterus is regarded by Iijima ('84, p. 419) as a simple gland whose secretions go to form the cocoon. In his opinion, it has no function in connection with the union of the sexual elements; he considers it homologous with the shell gland of Cestodes and Trematodes. According to Kennel ('88, p. 458), it is to be considered as a receptaculum seminis, and its secretions serve to preserve the spermatozoa. Hallez ('87, p. 24) maintains that fecundation takes place in the uterus, and that in it the yolk cells join the egg cells. According to Hallez, there is a division of labor among the cells lining the uterus. The majority of them secrete the substance of the cocoon, others secrete "un liquide

spécial" to support the vitality of the male elements, and possibly to aid in fecundation. He states that in Pl. polychroa the cocoon is produced in the uterus, but as regards Dendrocœlum lacteum he agrees with Iijima in maintaining that the cocoon is formed in the genital cloaca or atrium. In Phagocata I have found ova as well as spermatozoa in the uterus, and believe that fecundation takes place there. The spermatophores are deposited in the vagina and from there the spermatozoa make their way into the uterus. I believe also that a portion of the contents of the cocoon are secreted by the uterus, but that the substance of its wall, the shell, is produced from the glandular lining of the vagina, so that in Phagocata at least the "uterus" cannot be regarded as homologous with the shell gland of Cestodes. It is my purpose to discuss at length these questions, together with that of the formation of the spermatophore, in a subsequent paper on the embryology of this species.

No organ comparable with the "muskulösen Drüsenorgan" of Iijima ('84, p. 422), or the "vésicule (bourse) copulatrice" of Hallez ('79, p. 57, and '87, p. 20), is present.

Summary.

Phagocata differs from all known Triclads in possessing, besides a pharnyx which opens into the intestine at the junction of its three main trunks, many additional pharynges which are joined to the two lateral trunks of the intestine. The lateral pharynges are histologically identical with the median one; they differ from the latter only in size; the more remote they are from it, the smaller they are.

The rhabditi or dermal rods lie between the cells of the hypodermis, not in them. They are developed in cells lying in the sub-hypodermal mesenchyma; the cells are connected with the hypodermis by fine tubular prolongations. The connection of the parent cells of the rhabditi with the exterior is a primitive one, and the rods enter the hypodermis by emergence along these prolongations. The rhabditi are ultimately discharged from the hypodermis, and new ones are constantly being developed in new parent cells. They are slowly soluble in water, and are used for securing prey and for protection.

The parent cells of the rhabditi are unicellular glands, and the rods are their condensed secretions.

The "Stäbchenstrassen" of Rhabdocœles are homologous with the slime glands in Phagocata.

The basement membrane is a product of the hypodermis. It is structureless.

The pigment is intercellular, occurring in the form of scattered granules.

The pseudocœlar spaces of the mesenchyma are intercellular in origin, and sagittal muscles are directly continuous with processes of the mesenchyma cells.

The nervous system consists of a deeper and a superficial portion; a marginal nerve indirectly connects the two. The condition in Phagocata may be intermediate between that of Gunda and Rhynchodesmus.

The brain presents two commissures, an anterior and a posterior one, uniting the longitudinal nerve trunks. The so called "Substanzinseln" are intrusive connective tissue.

The testes give rise to tubular outgrowths, the vasa efferentia. The vasa deferentia have terminal enlargements and function as vesiculæ seminales.

The yolk glands arise by cell proliferation from two cell masses, the parovaria, which are in immediate contact with the ovaries. The intimate connection of the parovaria with the ovaries indicates the differentiation of the ovary and vitellarium from a common gland.

The so called uterus is not only a gland; it is a place in which the sexual elements are brought together, and where fertilization consequently takes place.

CAMBRIDGE, August, 1890.

It was not until this paper had gone to press that I had access to the recent work of Böhmig ('91) on Rhabdocœles. It was then too late for any detailed review. I am gratified to observe, however, that he has arrived at conclusions from his studies of Rhabdocœles which agree in many points with those which I have expressed in the foregoing paper, especially in his statements as to the fate and significance of rhabditi.

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EXPLANATION OF FIGURES.

All the figures are from camera drawings of Phagocata gracilis, Leidy.

ABBREVIATIONS.

atr.	Genital atrium.
cil.	Cilia.
cl. rhb.	Parent cells of the rhabditi.
cl. sp'z.	Parent cells of the spermatozoa.
com. a.	Anterior commissure of the brain.
com. p.	Posterior commissure of the brain.
com. t.	Transverse commissure.
con't. tis.	Connective tissue.
dt. sal.	Salivary duct.
e'th.	Epithelium.
e'th. ex.	External epithelium.
e'th. i.	Internal epithelium.
e'th. phy.	Epithelium of pharynx.
go'po.	Gonopore.
h'drm.	Hypodermis.
h'drm.'	Aborted cells of hypodermis.
in.	Intestine.
mb. ba.	Basement membrane.
ms'chy.	Mesenchyma.
mu. crc.	Circular muscles.
mu. crc. ex.	External circular muscles.
mu. crc. i.	Internal circular muscles.
mu. l.	Longitudinal muscles.
mu. l. ex.	External longitudinal muscles.
mu. l. i.	Internal longitudinal muscles.
mu. r.	Radial muscles.
mu. sag.	Sagittal muscles.
n.	Sensory nerve.
n. l.	Lateral nerve.
n. l.'a.	Anterior longitudinal nerve.
nl. con't. tis.	Nucleus of connective tissue.
nl. e'th.	Nucleus of epithelium.
n. l.'p.	Posterior longitudinal nerve.
nl. rhb.	Nucleus of parent cells of the rhabditi.
n. opt.	Optic nerve.
n. pi'ph.	Peripheral (marginal) nerve.
o.	Mouth opening.
oc.	Eye.
ov'dt.	Oviduct.
pe.	Penis.
phy. m.	Median pharynx.
phy. l.	Lateral pharynx.
plx. mu.	Nerves to muscular plexus.
rhb.	Rhabditi.
scc.	Secretions which do not form rhabditi.
sp'z.	Spermatozoa.
trn. i. a.	Anterior trunk of intestine.
trn. i. l.	Lateral trunk of intestine.
ut.	Uterus.
va. df.	Vasa deferentia.
vag.	Vagina.
vt'm.	Parovarium (vitellarium).
x.	Enlarged ends of vasa deferentia.

PLATE I.

Fig. 1. Portion of a longitudinal section of the dorsal wall of the body, showing the parent cells of the rhabditi and the position of the rhabditi in the hypodermis. × 900.

" 2. Cross section near the lateral margin of the dorsal side, in a region where there were no rhabditi, showing the hypodermis in its primitive condition. × 900.

In Figures 1 and 2 the basement membrane did not take the stain.

" 3. Longitudinal section through a region where there were many rhabditi which have been removed by partial maceration, showing the modified condition of the hypodermal cells due to the crowding of the rhabditi. × 900.

" 4. Longitudinal section of ventral wall of body, showing a young parent cell of the rhabditi, the nucleus almost filling the cell. The hypodermis removed. × 900.

" 5. Two parent cells of the rhabditi, from macerated material. × 960.

" 6. Longitudinal section of ventral wall showing two stages in the development of the parent cells of the rhabditi. Two small rhabditi have already been secreted in the larger cell. The hypodermis removed. × 900.

" 7. Stage in the development of the parent cells of the rhabditi next older than that shown in Figure 4. The cell has sunk deeper into the tissues, and the nucleus is smaller in relation to the size of the cell. Ventral wall of body, the hypodermis being removed. × 900.

" 8. Longitudinal section of ventral wall showing one of the rhabditi in the act of passing through the basement membrane. The hypodermis removed. × 900.

" 9. Showing the appearance of the rhabditi after having been acted upon by picric acid. × 900.

" 10. Longitudinal section of the ventral wall showing one of the parent cells of the rhabditi filled with the rods. The remnants of another cell represented by the nucleus and three rhabditi are seen close by The hypodermis has been removed. × 900.

Owing to a mistake of the lithographer, the nuclei of the parent cell (*nl. rhb.*) in Figure 10 are not represented as being granular, as they should be.

PLATE II.

Fig. 11. Cross section of an individual in the region of a young budding pharynx. Its connection with the intestine has not yet been established. × 300.

" 12. Portion of a cross section through one of the lateral pharynges. × 320.

" 13. A worm feeding on an Annelid; five of the pharynges are visible. Killed with hot corrosive sublimate while feeding. × 10.

" 14. Portion of a cross section through young pharynx, showing the nucleated epithelia. The other tissues are not yet differentiated. × 300.

" 15. Portion of a cross section through the vagina in the region where the musculature reaches its greatest development. × 120.

" 16. Longitudinal section of the wall of one of the smaller pharynges. × 500.

" 17. Portion of a longitudinal section through the slime glands in the head region, where they pass over the brain. × 300.

" 18. Portion of a cross section of the body to show the reticulated mesenchyma and its relation to sagittal muscles. × 500.

" 19 and 19*a*. Portions of the incipient yolk glands; in Figure 19 the nuclei are seen in process of division. × 820.

" 20. A partial reconstruction of the whole worm showing the pharynges and their relation to the intestinal tract. × about 20

" 20*a*. Outline to show the appearance of the living worm while in progression. × 9.

" 20*b* and 20*c*. Outlines showing forms assumed by the worm when at rest. × 6.

" 21. Longitudinal section through the ovary and parovarium showing their relation to each other. × 300.

" 22. Section through a parovarium at the time when the yolk glands are beginning to develop. From the same individual as Figures 19 and 19*a*. × 820.

" 23. Cross section through the vas deferens. × 300.

" 24. Portion of a section which passes through one of the testicular sacs, showing its tubular outgrowth, — vas efferens × 300.

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PLATE III.

Fig. 25. Horizontal section through the head region showing the brain and sensory nerves, and the relation of the anterior longitudinal nerve to the marginal nerve (*n. pi'ph.*). The right-hand side of the section is a little more dorsal than the left. × 52.

" 26–31. From a series of cross sections through the brain region. The sections are taken at intervals of 60 μ. Figure 26 is the most anterior. × 52.

" 32–36. From a series of horizontal sections through the brain region, cut from the dorsal side. The sections are consecutive, and 30 μ in thickness. × 52.

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PLATE IV.

Figs. 37 and 38 Two consecutive horizontal sections (30 μ in thickness) from the ventral side passing through the floor of the pharyngeal chamber. Figure 37 is the more ventral, and shows the marginal nerve; the relation of the latter to the longitudinal trunks is evident upon comparing Figures 37 and 38. $\times$ 27.

" 39 and 40. Two longitudinal sections, parallel with the sagittal plane, through the brain region. $\times$ 52.

" 41. From an isolation preparation, showing one of the sub-hypodermal glands from the region of the gonopore. $\times$ 700.

" 42. A view of the sexual organs showing their relations to one another. The figure was accidentally inverted by the lithographer, thus bringing the posterior end uppermost. Partially diagrammatic. $\times$ 35.

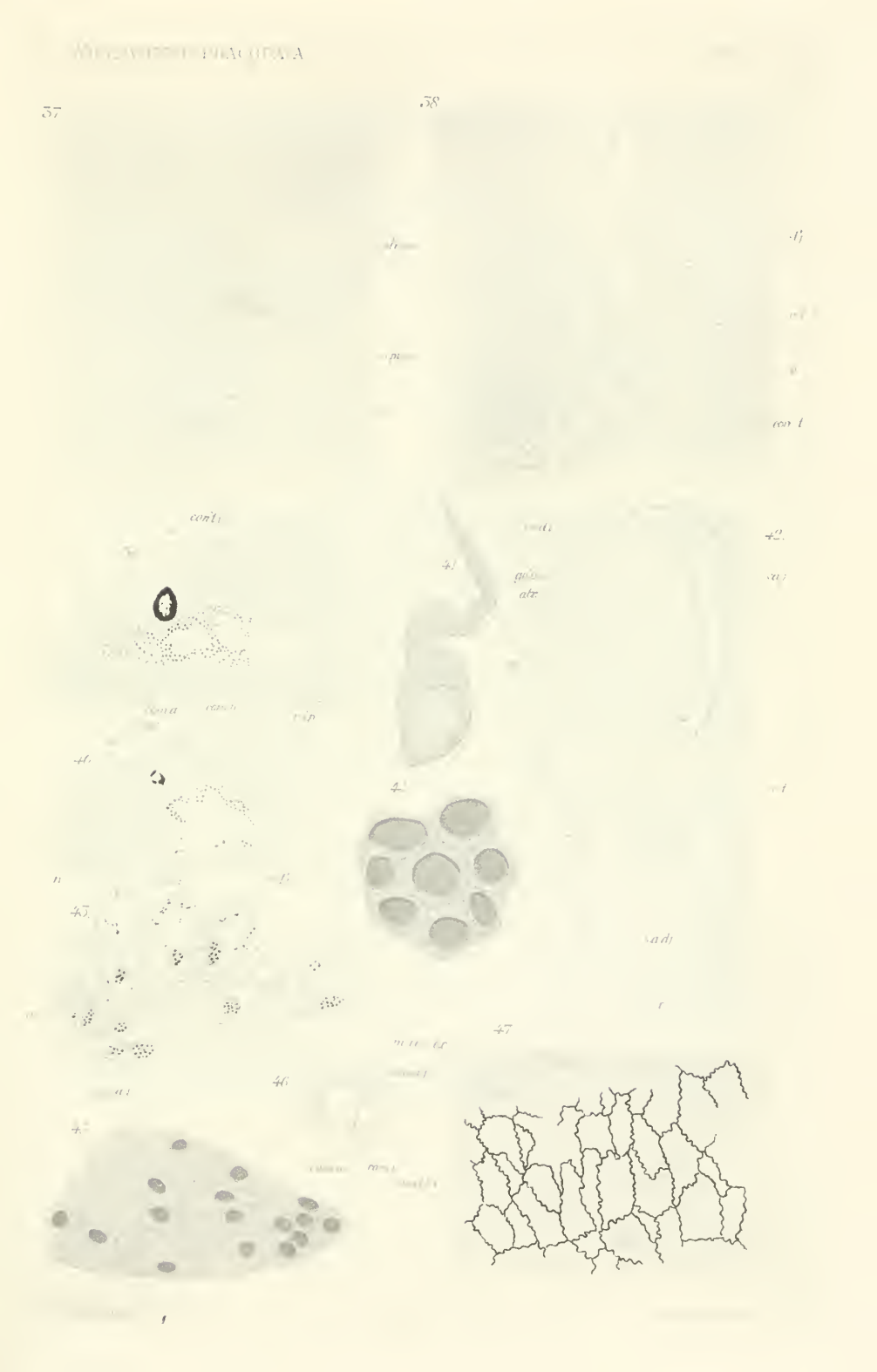
" 43. Portion of a cross section of one of the lateral branches of the intestine. $\times$ 450.

" 44. Portion of a section through a parovarium of an individual in which the yolk glands were fully developed. $\times$ 680.

" 45. Section through a portion of a yolk gland from the same individual as Fig. 44. $\times$ 260.

" 46. Sagittal section through the brain, showing the two commissures. $\times$ 60.

" 47. Portion of a tangential section of one of the pharynges, to show the cell boundaries of the external epithelium. From an isolated pharynx killed in hot silver nitrate. $\times$ 350.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No. 2. — *The Compound Eyes in Crustaceans.* By G. H. Parker.[1]

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Introduction.

Some four years ago, at the suggestion of my instructor, Dr. E. L. Mark, I began the investigation of the compound eyes in Crustaceans. In order to familiarize myself with the subject, I determined to study at first in detail the structure of the eyes in a single species, and for this purpose I turned my attention to our common lobster, Homarus americanus. My results were published in a paper entitled "The Histology and Development of the Eye in the Lobster." Since the publication of that paper, I have had the opportunity of examining the eyes in a number of other Crustaceans, and my observations and conclusions concerning these eyes are contained in the following pages.

The *material* which I have used in the present study was in part supplied to me through the kindness of several friends, and in part collected by myself. Of that which I obtained myself, some was gathered in the immediate vicinity of Cambridge, but much of it came either from Wood's Holl, Mass., or from Newport, R. I. The material which I obtained at Newport was collected at the Newport Marine Laboratory during the summer of 1890, and consisted of specimens of Idotea, Evadne, and Pontella; that which I got at Wood's Holl was collected at the United States Fish Commission Station during a brief period

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXV.

which I spent there in the summer of 1889, and included much of the material which I used in studying the eyes of Decapods. For the opportunities of collecting, both at Newport and Wood's Holl, I am indebted to Dr. Alexander Agassiz. I also desire to express my thanks to Prof. M. McDonald, the United States Commissioner of Fish and Fisheries, for many courtesies shown me while at the government station at Wood's Holl.

Essentially the same *methods* as those which I used in investigating the eyes in the lobster were employed in studying the eyes in other Crustaceans. As these methods have been described at some length in my paper on the lobster's eye (Parker, '90[a], pp. 3, 4), further mention of them in this connection is unnecessary.

Before proceeding to an account of the eyes in Crustaceans, a few statements should be made concerning the use of terms. In the following anatomical descriptions, I have very generally adhered to the older and more established terms. It must be admitted that some of these, on account of their derivation, are not entirely satisfactory, but because of their general acceptance I have chosen to retain them rather than to attempt to replace them by new ones.

The term *retinula*, the use of which varies with different writers, was introduced by Grenacher ('77, p. 17), who employed it to designate the rhabdome and the group of cells by which this structure is surrounded. Subsequently, Patten ('86, p. 544) used the same term as a name for a single cell of the group to which Grenacher gave the name retinula. In my paper on the eyes of the lobster I followed Patten's usage, but in the present paper I have decided to employ the term as originally defined by Grenacher, and to designate the individual cells in the retinula as *retinular cells*, — a translation of the term already used for this purpose in many German publications.

The greater part of the present paper is taken up with descriptions of the eyes in different Crustaceans. The amount of detail thus collected is considerable, and might appear at first sight to include many unimportant particulars; but the number of observations recorded is justifiable, I believe, on the ground that the majority of them bear more or less directly upon the solution of the principal question dealt with in the paper.

The following statements will make clear the character of this question. It is now well recognized that the retina in compound eyes is composed of a number of similar units or ommatidia, and that each ommatidium consists of a cluster of cells regularly arranged around a

central axis. With very few exceptions, the different ommatidia in the retina of any given Crustacean agree with one another in the number and arrangement of their cells; in other words, in a given retina any ommatidium is the structural duplicate of any other. This uniformity suggests the idea of a structural type, and already a number of such types have been described. Some of these find representatives apparently only in the ommatidia of a single species, but more frequently the type characterizes a genus, family, or even a sub-order. Types differ from one another, either in the number of their cells or in the arrangement of these cells. Of these differences, the one which involves a variation in the number of cells is the more fundamental. This difference, however, has probably arisen by the gradual modification of an ancestral type, and, granting this, it follows that the ommatidia of one type are genetically connected with those of other types. This leads directly to the statement of the principal question, namely, *What are the means by which ommatidial types are modified, and what is the significance of the changes through which these types pass?*

This question, although easily stated, is not so easily answered; the facts presented in the following pages cannot be said to settle it, and yet they seem to me to increase materially the possibilities of its solution.

A partial answer to at least the first portion of the question has already been suggested (Parker, '90[a], pp. 56–58); it can be briefly stated as follows. There is reason for believing that those ommatidia which are composed of a small number of cells more closely resemble the ancestral type than those composed of many cells. Granting this statement, one would naturally expect that the more complex ommatidia had been derived from the simpler ones by an increase in the number of their elements. Perhaps the most natural method by which this increase could be accomplished would be by the further division of the cells already forming the ommatidium. Consequently, cell division in this sense seemed to me to afford a sufficient means for the modification of ommatidial types. In the present paper it is in part my purpose to show precisely to what extent cell division can be said to have modified ommatidia, and to determine whether any other factors have been involved in this process.

The Retina.

The retina in those Crustaceans in which its development has been studied originates as a thickening in the superficial ectoderm. At least

three types of retinal structure can be distinguished, depending upon the ultimate form which this thickening assumes.

The FIRST TYPE which will be described is in several particulars the simplest, and probably represents a primitive form from which the other two are derived. This type is characteristic of the eyes in Decapods, Schizopods, Stomatopods, Isopods, the Nebaliæ, and the Branchiopodidæ, and is represented by a simple thickening in the superficial ectoderm.

Branchiopodidæ. — In the eye of adult specimens of Branchipus the retina is a lenticular thickening occupying the inner concavity of the distal end of the optic stalk. Near its edges the retina is directly continuous with the adjoining hypodermis. Its proximal face is bounded by a basement membrane which is also continuous with the corresponding membrane of the hypodermis, and its distal face is closely applied to the inner surface of the superficial cuticula. Thus the retina in the adult has in every respect the appearance of a simple thickening in the hypodermis.

The way in which the retina originates in Branchipus confirms the opinion that this organ has the simple structure suggested in the foregoing paragraph. The development of the retina in this genus has been studied by Claus ('86, p. 309), whose account can be summarized as follows. In that part of the head from which the optic stalks eventually arise, the ectoderm becomes considerably thickened; this thickening is subsequently divided into a superficial and a deep portion; the latter sinks into the head and becomes a part of the central nervous system; the former retains its external position and is converted into the retina. In Branchipus, therefore, the retina originates as a simple ectodermic thickening which retains its superficial position throughout the life of the individual. This method of origin, and the position permanently retained by the retina, are the two principal characteristics of the first retinal type.

Isopoda. — In adult specimens of Idotea irrorata, as sections perpendicular to the external surface of the eye show (Plate V. Fig. 49), the retina bears the same relation to the hypodermis as it does in Branchipus. Similar structural relations occur also in the eyes of Idotea robusta and of young specimens of Serolis Schythei.

The development of the retina in Isopods has been observed by Dohrn and Bullar. As early as 1867, Dohrn ('67, p. 256) described the eye in Asellus as originating in connection with a thickening in the lateral wall of the head, presumably in the ectoderm of that region. The de-

tails of the development of this organ were not followed on account of the continual increase of pigment. Bullar ('79, pp. 513, 514) in a paper on parasitic Isopods described the development of the retina in Cymothoa. His account is substantially as follows. In the course of the development of the cerebral ganglion, when this structure is separated from the superficial ectoderm, the latter remains on the exterior of the embryo as a layer of considerable thickness. From this superficial layer is developed the retina, i. e. all parts of the eye which in the adult lie between the basement membrane and the corneal cuticula.

I have studied a few stages in the development of the eyes in Idotea robusta. The retina in this species originates as a simple thickening in the superficial ectoderm, in essentially the same manner as Bullar has observed in Cymothoa.

The retina in Isopods, both in respect to its method of development and its general structure in the adult, is unquestionably a representative of what I have called the first type of retinal structure.

Nebaliæ. — In Nebalia, as the figures given by Claus ('88, Taf. X. Figs. 8 and 17) show, the retina and adjoining hypodermis are directly continuous, and the former presents all the characteristics of a simple thickening in the hypodermis.

Stomatopoda. — In an adult specimen of Gonodactylus which I examined, the relation between retina and hypodermis was the same as in Nebalia.

Nothing is known, I believe, of the development of the retina in either the Nebaliæ or the Stomatopods. The structure of the eyes in the adults of both groups, however, shows very conclusively that their retinas belong to the same structural type as those of Branchipus.

Schizopoda. — In describing the development of Mysis chamelio, Nusbaum ('87, pp. 171–185) states that the retina arises from a thickening in the superficial ectoderm, and adds that its formation, so far as his observations extended, was not complicated by an involution.

In Mysis stenolepis, a Schizopod whose eyes I have studied, the retina and hypodermis in the adult are directly continuous, as in Branchipus. This relation is what would be expected from the method of development described by Nusbaum.

Decapoda. — Carrière ('85, p. 169), in his account of the eyes in Astacus, showed very clearly that in the adult the retina and hypodermis formed a continuous layer. This relation was subsequently observed by me in Homarus (Parker, '90[a], p. 5), and I have since seen the same condition in Gelasimus, Cardisoma, Cancer, Hippa, Palinurus, Pagurus,

Cambarus, Crangon, and Palæmonetes. There is, therefore, considerable ground for the support of Carrière's generalization, that the relation of the retina to the hypodermis as shown in Astacus is characteristic of all Decapods.

The development of the retina has been more fully studied in Decapods, perhaps, than in any other group of Crustaceans. Nevertheless, the accounts given by various writers are by no means in agreement, but differ in several important particulars. In a former paper (Parker, '90[a], pp. 31–43), I devoted considerable space to the discussion of these accounts, and I shall therefore not reopen the subject here. Suffice it to say, that since the publication of the paper referred to nothing has transpired to alter my belief that the retina in Decapods originates as a simple thickening in the superficial ectoderm.

In a recent preliminary communication by Lebedinski ('90) on the development of a marine crab, Eriphya, a brief description of the origin of the eye is given. This description, however, is so very much condensed that it is not easily understood, and since the author himself confesses that, on account of the complexity of the subject, a description without figures must be almost unintelligible, it would be unwise to hazard a presentation of his views. I shall therefore pass over this paper without further comment.

The evidence advanced in the course of the preceding paragraphs leaves no doubt in my mind that the retinas in the Branchipodidæ, the Nebaliæ, the Isopods, Stomatopods, Schizopods, and Decapods, belong to the same structural type, and that this type is represented by a thickening in the external ectoderm (hypodermis), which retains permanently its superficial position.

The SECOND RETINAL TYPE is more complicated than the first, and differs from it in that the retina does not retain its position at the surface of the body, but becomes buried beneath a fold of integument. Our knowledge of this type is largely due to the researches of Grobben ('79). The type is represented in the eyes of the Apusidæ, the Estheridæ, and the Cladocera.

Estheridæ. — In adult specimens of Limnadia Agassizii the two lateral eyes are rather closely approximated, and occupy a position in the ventral anterior portion of the animal's body (Plate IV. Fig. 33). The relation of the eye to the surface of the body can be seen most satisfactorily in sagittal sections. In such a section (Fig. 35) the eye has the appearance of a stalked structure which projects anteriorly into a cavity, the optic pocket (*brs. oc.*); this pocket communicates with the

exterior by means of a small opening (*po. brs.*), the optic pore. The free surface of the stalked portion of the eye is covered with a delicate cuticula, which, after being reflected from the base of the stalk over the inner surface of the wall of the pocket, becomes continuous at the pore of the pocket with the superficial cuticula. The retina (Fig. 35, *r.*) occupies the greater portion of the optic stalk. Its distal face is bounded by the delicate cuticula already mentioned, and its proximal face is limited by a basement membrane (*mb. ba.*). This membrane becomes indistinct as the base of the stalk is approached, but the retina itself is apparently continuous in this region with the layer of cells which rests on the cuticular wall of the optic pocket, and which finally unites at the pore of the pocket with the superficial hypodermis. Thus the retina may be said to be continuous with the hypodermis.

The structure of the eyes in Limnadia Agassizii is such that they can be described as stalked eyes which have been surrounded by a fold of the integument, so as to become enclosed within a space, the optic pocket, which communicates with the exterior only by means of the optic pore.

An eye of essentially this structure has been described by Grobben ('79, p. 255) in Limnadia Hermanni, Limnetis brachyurus, and Estheria ticinensis, and in the last genus enough of the development of the eye was observed to indicate that the optic pocket was formed by the growth of a fold of integument over the optic stalk.

Apusidæ. — In Apus, according to Grobben ('79, p. 256), the plan of the eye is essentially similar to that in the Estheridæ. The eyes project into an open pocket, the cavity of which permanently communicates with the exterior. Judging from the figure given by Claus ('86, Taf. VII. Fig. 11, compare p. 366), the right and left retinas in Apus are not so close to one another as in the Estheridæ (compare Plate IV. Fig. 34).

Cladocera. — The structure and development of the retina in the Cladocera has been carefully studied by Grobben. My own observations on this group have been limited to a single genus, Evadne, and as this genus is not very favorable for the determination of the general relations of the retina I must rely almost entirely upon Grobben's descriptions.

In the development of Moina, according to Grobben ('79, p. 253), the retinal thickening is covered by a fold of the integument in such a manner that an open optic pocket is produced, as in Limnadia. By the closure of what corresponds to the optic pore, this pocket eventually

loses its connection with the exterior, and becomes reduced to a closed sac on the distal face of the retina. With the closure of the sac, the continuity of the retina with the superficial hypodermis becomes interrupted.

In other Cladocera, especially the genera Sida and Daphnia, Grobben has found evidence to believe that the eyes are of essentially the same structure as in Moina. In a majority of the Cladocera the two compound eyes coalesce even more completely than in Limnadia.

In the development of Moina, as the preceding description indicates, the eye passes through a phase which closely resembles the permanent condition in Limnadia. The eye in the latter may therefore be interpreted as representing a stage in the phylogeny of the eye in Moina.

In accordance with the facts presented in the foregoing account, the second retinal type can be described as one in which the retina does not retain its primitive external position, but sinks below the surface of the animal and becomes covered by a fold of the integument. The optic pocket thus formed may remain permanently open, as in the Apusidæ and Estheridæ, or may become closed and partially obliterated, as in the Cladocera. The right and left retinas either remain separated, as in the Apusidæ, or become closely approximated, as in the Estheridæ, or fused, as in the Cladocera.

The minor modifications which this retinal type presents are not without importance. Bearing in mind the general statement that the compound eyes in Crustaceans are separate, paired, superficial structures, it is evident that the eyes in the Apusidæ, in which the retinas are separate and the optic pocket permanently open, depart only slightly from the primitive condition. In the Estheridæ, in which the two retinas are closely approximated, the eye is farther removed from the original type; but not so far as in the Cladocera, in which not only the two retinas are fused, but the optic pocket is closed and partially obliterated, thus entirely disconnecting the retina from the hypodermis. The three groups — the Apusidæ, the Estheridæ, and the Cladocera — may consequently be taken to represent a series in the differentiation of the second retinal type. That this series is a natural one, and that it culminates in the Cladocera, is shown from the fact that in the development of Moina, and perhaps many other Cladocera, the eyes pass through stages which reproduce the essential features of the permanent condition in the Apusidæ and Estheridæ.

In the THIRD RETINAL TYPE, as in the more differentiated form of the second, the retina is completely separated from the hypodermis.

The method by which the separation is here accomplished is not by the closure of an involution, as in the second type, but by a process the nature of which will be described in the following pages. The third type is represented by the eyes in Amphipods, and possibly in Copepods.

Amphipoda. — The peculiar relation which the retina bears to the hypodermis in Amphipods can be easily seen in Gammarus. In this genus, as Carrière ('85, pp. 156–160) has clearly demonstrated, the retina lies immediately below the hypodermis, and is separated from the latter by a well defined structure, the corneo-conal membrane (Fig. 1, *mb. crn'con.*). This membrane, although visible with perfect clearness, is nevertheless extremely delicate, and has the appearance of a single lamella. I believe, however, that its structure is more complex, and that it is composed of two very intimately united membranes, one of which is produced by the retina, the other by the corneal hypodermis. This belief is based upon the fact that at the edge of the retina the apparently single membrane separates into what may be considered its two constituents. One of these becomes the basement membrane of the general hypodermis, and the other, which I have called the capsular membrane, passes over the edge and proximal face of the retina, and is finally reflected over the optic nerve (Fig. 1, *mb. n. opt.*). In addition to the capsular membrane, the eye in Gammarus possesses still another membrane (Fig. 1, *mb. ba.*). This is a delicate lamella, which is approximately parallel to the deep face of the eye at a level between the rhabdomes and retinular nuclei (compare Fig. 2), and which consequently divides the space within the capsular membrane into two chambers, a larger distal and a smaller proximal one. At its periphery this intercepting membrane unites with the capsular membrane.

The corneo-conal and capsular membranes in Gammarus show no evidence of being perforated, but together constitute a closed capsule, which separates the retina from all adjoining tissues except the optic nerve. Both membranes are composed apparently of a homogeneous substance, in which I have never been able to distinguish any trace of cells. It is therefore probable that these membranes are cuticular.

The intercepting membrane, unlike either the capsular or the corneo-conal membrane, is pierced by a great number of holes, through which the proximal ends of the retinular cells project. This membrane, therefore, has the form of a meshwork. According to Carrière ('85, p. 158) it is composed of numerous connective-tissue cells, but this statement is not confirmed by my own observations. In depigmented sections of

the retina the intercepting membrane had the appearance of a delicate lamella, in which I was unable to find any trace of cells. Not unfrequently the nuclei of certain accessory pigment cells (Fig. 2, *nl. h'drm.*) appear to touch the membrane, and even at times to lie with their long axes parallel to it, but in no case could these nuclei be said to be *in* the membrane. In sections of the retina from which the natural pigment had not been removed, it was often difficult to decide whether a given nucleus was *in* the membrane or only *next to* it. Possibly appearances such as these have led Carrière to believe that the membrane was cellular. My own opinion is, that the intercepting membrane, like the other two membranes, is a cuticula, and does not contain cells.

From the foregoing account, it will be seen that in an adult Gammarus the retina lies immediately under an undifferentiated corneal hypodermis, and is enclosed, excepting where the optic nerve emerges from it, by a non-perforated cuticular capsule. The space within this capsule is divided by a perforated cuticular membrane into a large distal and a small proximal chamber.

In Hyperia, judging from the figure given by Carrière ('85, p. 161, Fig. 123), the retina has essentially the same structure as in Gammarus. The intercepting membrane is in a position proximal to the rhabdomes and distal to the retinular nuclei. The layer of pigment cells, which Carrière ('85, p. 161, Fig. 124) apparently considers the intercellular membrane itself, in my opinion marks only approximately the position of that membrane. Probably in Hyperia, as in Gammarus, these cells rest on the distal face of the intercepting membrane.

In Phronima each side of the head is occupied by two eyes, instead of one, contrary to the condition in the more typical Amphipods. Of the two eyes, one is dorsal, the other lateral. This difference in position affords a convenient means of distinguishing them. The lateral eye presents all the essential structural features of the single eye in Gammarus (compare Carrière, '85, Figs. 125 and 121). The dorsal eye, although differing considerably in shape from the lateral one, is nevertheless constructed upon the same morphological plan. Its most important peculiarity is the shape of its intercepting membrane and the adjoining structures. In the dorsal eye the intercepting membrane, instead of lying in a plane nearly parallel with the external surface of the retina, as in the lateral eye, is cone-shaped. The axis of this cone corresponds to the axis of the eye; its apex is near the brain, and its base faces the external surface of the eye (compare Claus, '79, Taf. III. Fig. 20, and Taf. VII. Fig. 58). The ommatidia are arranged approximately parallel

to its principal axis; distally, they terminate in the region of its base; proximally, they end either at its apex or on its lateral walls near the apex. The rhabdomes lie within the cavity of the cone, i. e. they are distal to the intercepting membrane, as in other Amphipods. The retinular nuclei cover the apical portion of the external surface of the cone, i. e. they are proximal to this membrane. These nuclei are covered externally by a second cone-shaped membrane, which separates them from the surrounding tissue. This membrane occupies the position of the capsular membrane of other Amphipods, and is unquestionably homologous with it.

The fact that both the lateral and dorsal eyes in Phronima are constructed upon the same plan as the single eye in Gammarus, supports the view that these two eyes have arisen by the division of a primitively single retina into two parts, and the subsequent independent differentiation of each part.

As the preceding account shows, in all Amphipods whose eyes have been studied carefully, the retinas conform to one structural type well exemplified by Gammarus. In this type the retina is characterized by two peculiarities: first, it is not continuous with the hypodermis, but lies immediately below that layer; and secondly, it possesses what appear to be two basement membranes, the capsular and the intercepting membranes. The significance of these peculiarities will be discussed in the following paragraphs.

The separation of the retina from the hypodermis is characteristic of only the more mature conditions of the eye in Amphipods; for as Pereyaslawzewa ('88, p. 202) has shown in Gammarus, and Rossiiskaya ('89, p. 577, and '90, p. 89) has demonstrated in Orchestia and Sunamphitoë, the retina originates as a thickening in the superficial ectoderm, in the same manner as in the majority of Crustaceans. So far as I am aware, however, no one has observed the detachment of the retina from the hypodermis, a process which must take place before the adult condition is reached. In the figure of the developing eye in Gammarus given by Pereyaslawzewa ('88, Plate VI. Fig. 120), the distal portion of the retinal thickening contains almost nothing but developing cones. In sections of my own from a corresponding region in a young specimen of Gammarus, the distal portion of the retina contains not only developing cones, but also isolated nuclei, which occasionally lie between the cones, but more frequently occur in positions distal to them. These nuclei are as numerous in the centre of the distal face of the retina as on its edges, and at this stage can always be easily distinguished from the nuclei of the cone

cells. I believe they represent the nuclei of the corneal hypodermis. The retina proper is probably separated from this hypodermis by delamination; at least, the corneo-conal membrane is formed at a stage slightly older than that last mentioned, and, judging from the appearances at this stage, its formation is not accompanied by any folding of the hypodermis or retina, but is the result of a differentiation in place. Unfortunately, none of the specimens which I studied showed any steps in the formation of the corneo-conal membrane, and I am therefore uncertain as to the exact method of its growth.

Of the two membranes in the basal portion of the retina of Gammarus, presumably only one corresponds to the basement membrane of other Crustaceans. The position occupied by the two membranes, as well as their structure, serves to indicate which is the true basement membrane. At first sight one might suppose that the capsular membrane, at least in its proximal portion, corresponds to the basement membrane, but this interpretation is not probable, for the reason that the capsular membrane is not pierced by the fibres of the optic nerve, a characteristic of the true basement membrane of the eye. I therefore believe that the intercepting membrane, since it is perforated by these fibres, is the homologue of the basement membrane, and that that portion of the capsular membrane which might be regarded as a basement membrane is in reality merely the cuticular sheath of the optic nerve.

So far as I can foresee, the only objection to be urged against this interpretation of the intercepting membrane is found in its relation to the retinular nuclei. These nuclei in the eyes of almost all other Crustaceans lie on the *distal* side of the basement membrane. Granting that the intercepting membrane is the basement membrane, one must admit that in Amphipods they lie on the *proximal* side of this membrane. This admission might at first sight appear to offer an obstacle to the homology which I have suggested; but it can be made with consistency, I believe, provided one can show that the position of the retinular nuclei is not necessarily fixed. That such is the case is evident from the following facts. In Decapods the retinular nuclei usually occupy a position in their cells distal to the rhabdome. In Porcellio, as Grenacher ('79, Taf. IX. Fig. 96) has shown, they have a more proximal position, lying in the same transverse plane as the rhabdome itself. In Serolis they are midway between the rhabdome and the basement membrane. These conditions show, I believe, that the retinular nuclei may occupy very different positions in their cells, and that the step from the condition shown in Decapods to that shown in Serolis is not greater than that

from Serolis to the Amphipods. It seems to me, therefore, that the objection suggested at the beginning of this paragraph is almost without weight. This conclusion, moreover, is supported by the fact that in Idotea (Plate V. Fig. 49) the retinular nuclei lie proximal to the basement membrane, whereas in the majority of other Isopods they are distal to that membrane.

From the preceding discussion, I conclude that the retina in Amphipods originates as a simple thickening in the superficial ectoderm, and that this thickening subsequently becomes separated, probably by a process of delamination, into a deeper portion, the retina proper, and a more superficial portion, the corneal hypodermis. The latter alone retains its original connection with the adjacent hypodermis. Of the two membranes present in the basal portion of the eye in Amphipods, that which I have called the intercepting membrane is homologous with the basement membrane of the retina in other Crustaceans, and that which has been designated as the capsular membrane is in large part the cuticular sheath of the optic nerve.

Copepoda. — The retinas in the Branchiura and Eucopepoda, the two divisions of the Copepods, present such different structural conditions that for purposes of description it is better to consider them separately.

Branchiura. — In adult specimens of Argulus, the retina is completely separated from all surrounding tissue, excepting the optic nerve, by an intervening blood space (Plate II. Fig. 11, *cœl.*). This peculiar condition was first clearly described by Leydig ('50, p. 331), although as early as 1806 Jurine ('06, p. 447) remarked that the eye in this genus was contained in a transparent membranous sac, which apparently contained a fluid, and Müller ('31, p. 97) some twenty-five years later described the retina as separated from the "cornea" by an intervening space filled with fluid. It remained, however, for Leydig to determine the extent of this space, and to demonstrate that the fluid which it contained was blood. The more essential features of Leydig's description have since been confirmed by Claus ('75, pp. 254–256).

The development of the eye in Argulus has not been studied with sufficient fulness to allow one to determine the relation of its retina to the hypodermis. But from the strong resemblance which the eye in the adult bears to that in Amphipods, it is probable that the course of development in the two cases is not unlike. Probably the retina in Argulus originates as a thickening in the superficial ectoderm, and subsequently not only suffers delamination, as in the Amphipods, but becomes actually withdrawn from the superficial layer (corneal hypodermis).

If this course of development really takes place, the various structures in the eye of an adult Argulus can be easily homologized with those in Amphipods. Thus the corneal hypodermis and corneal cuticula of Amphipods would probably be represented by the hypodermis and cuticula dorsal to the eye in Argulus (Fig. 11). The basement membrane of this hypodermis would correspond to the corneal component of the corneo-conal membrane of Amphipods, and the conal constituent would be represented by what is called the preconal membrane in Argulus (Fig. 11, *mb. pr'con.*). Proximally, the preconal membrane becomes continuous with the sheath of the optic nerve (Fig. 11, *mb. n. opt.*), the equivalent of the capsular membrane of Amphipods. The basement membrane of the retina in Argulus, as in Amphipods, is the membrane pierced by the fibres of the optic nerve (Fig. 11, *mb. ba.*).

Grobben ('79, p. 258) has suggested that possibly the eye in Argulus is of the same type of structure as in Phyllopods, but I do not share in this opinion for the following reasons. In Estheria, the delicate cuticula which covers the optic stalk is morphologically a portion of the outer surface of the body, and, as I hope to show subsequently, is subtended by a true corneal hypodermis. There is no corneal hypodermis beneath the preconal membrane of Argulus. Moreover, there is nothing in the eye of Argulus to correspond to the optic pocket of the Estheridæ, or to the optic sac of the Cladocera, except the circumretinal blood space, and it seems to me very improbable that this space was once a cavity in communication with the exterior, and afterwards became converted into a blood space. I therefore believe that the plan of the eye in Argulus is not similar to that in the Phyllopods, but rather that it represents a modification of the type presented by the Amphipods. The satisfactory determination of this question can be settled, however, only by embryological evidence.

Eucopepoda. — In adult specimens of those true Copepods which possess rudiments of the lateral eyes, — the Pontellidæ and Corycæidæ, — the retina is apparently separated from the hypodermis. In the Corycæidæ it usually lies at some considerable distance from the hypodermis, and in Pontella the two structures, although near one another, are nevertheless not continuous.

The development of the lateral eyes in the Corycæidæ and Pontellidæ has not been studied, and consequently it cannot be stated with certainty whether the retinas in these Crustaceans originate from the hypodermis or not. In the metanauplius larva of Cetochilus, a Copepod which as an adult has no lateral eyes, Grobben ('80, p. 262) has de-

scribed a pair of thickenings, which extend from the superficial ectoderm of the antero-lateral part of the head to the brain. These thickenings are present only in the early stages of development, and represent the unsevered connection between the brain and the superficial ectoderm. They closely resemble the developing lateral eyes of Branchipus, and Grobben has therefore very justly considered them rudiments of the lateral eyes. If the rudiments of the lateral eyes in Cetochilus develop from the superficial ectoderm, it is probable that the lateral eyes in other Copepods have a similar origin.

To which of the three retinal types already described the eyes in Copepods belong is not easily decided. The absence of any indication of an optic pocket, either in the development of what Grobben considers the rudiments of the lateral eyes in Cetochilus, or in the fully formed eyes in other genera, seems to me to preclude the possibility of these eyes belonging to what I have described as the second type. The separation of the retina from the hypodermis prevents them from being classed with the first type, and, especially in the case of the Branchiura, brings them into close relation with the third type. It is my opinion, that, if the lateral eyes in Copepods are not representatives of a fourth type, essentially different from the three already described, they must be considered members of the third retinal type.

Certain species of Cumaceæ, Ostracods, and Cirripeds possess optic organs which probably represent the compound eyes of other Crustaceans; but so far as I am aware, the relation of these structures to the hypodermis is unknown. It is therefore impossible to state whether those eyes represent other retinal types, or belong to one of the three already described.

According to the preceding account, three retinal types can be distinguished in the compound eyes of Crustaceans. In the first of these the retina is a simple thickening in the superficial ectoderm (hypodermis). This type is characteristic of the eyes in Isopods, the Branchiopodidæ, the Nebaliæ, Stomatopods, Schizopods, and Decapods. In the Isopods, the eyes are sessile; in the other groups of the first type, they are borne on the distal ends of movable optic stalks.

In the second type, although the retina, as in the first type, originates as a thickening in the superficial ectoderm, it ultimately becomes enclosed within an optic pocket. This may remain permanently open, as in the Apusidæ and Estheridæ, or it may become closed, as in the Cladocera. In the Apusidæ, so far as I am aware, the eyes are not

capable of motion, and in the Estheridæ they are, if at all, only slightly movable. In the Cladocera, where the second type probably reaches its greatest differentiation, the retina is remarkable for the freedom of its motion.

In the third type the retina originates from thickened hypodermis, which subsequently separates into two layers, the corneal hypodermis and the retina proper (a layer of cones and retinulæ). This separation is accomplished either by the formation of a corneo-conal membrane, as in Amphipods, or by what I believe to be an actual withdrawal of the retina proper from contact with the hypodermis, as in Copepods. Only in the representatives of the extreme modification of this type, the Copepods, are the eyes movable.

The course of development taken by each of the three types very clearly indicates their mutual relations. Evidently the first type is a primitive one, and since the first steps in the development of the second and third reproduce the permanent condition of the first, these two may therefore be considered derivatives from the first. It is interesting to observe that in the simpler condition of each type the retina is fixed, whereas in the more differentiated form it has become movable. The sinking of the retina into the deeper parts of the body, as represented in the second and third types, may have been induced by the protection thus obtained for the eye. After the three types were differentiated, each one seems to have been modified in a special way to give rise to a movable retina.

Arrangement of the Ommatidia.

The ommatidia in the retinas of some Crustaceans are so few in number that they can scarcely be said to be grouped according to any system. Where they are numerous, however, they are arranged upon one or the other of two plans. These may be designated the hexagonal and tetragonal plans of arrangement. In the hexagonal plan the imaginary outline of the transverse section of an ommatidium is a hexagon, and each ommatidium, excepting those on the edge of the retina, is surrounded by six others. In the tetragonal arrangement the ideal transverse section of an ommatidium is a square. Each of the four sides of this square is occupied by one of the four faces of an adjoining ommatidium.

The arrangement of the ommatidia can usually be determined by a careful inspection of the external surface of the eye; this determination is considerably facilitated by the presence of a facetted cuticula. Sometimes the form of a single facet is sufficient to indicate the plan of

arrangement. Thus, hexagonal facets have never been observed except in connection with the hexagonal plan of arrangement. Circular facets are likewise known to occur only with this method of grouping. Square facets, on the other hand, may accompany either the hexagonal or tetragonal arrangement of deeper parts.

The hexagonal arrangement is apparently characteristic of the ommatidia in all Crustaceans,[1] except the Decapods. In the Decapods, as will be shown presently, the ommatidia are arranged either upon the hexagonal or the tetragonal plan. Before proceeding, however, to a description of the arrangement of the ommatidia in Decapods, it would be well perhaps to call attention to the rather peculiar grouping of these structures in Gonodactylus, a Stomatopod.

For a clear understanding of the arrangement of the ommatidia in this Crustacean, it is necessary to have some previous knowledge of the shape of its optic stalk. In Gonodactylus the stalks are elongated cylinders, the distal ends of which are rounded. In alcoholic specimens the stalks in an undisturbed position rest with their longitudinal axes approximately parallel with the chief axis of the animal, and with their distal ends directed forward. The retina occupies the free end of the stalk. Dorsally it extends over the distal half, ventrally over only the distal third of the stalk.

The ommatidia in Gonodactylus are of two kinds, large and small, which are always easily distinguishable from each other, although they differ in no essential respect except size. The large ommatidia are definitely arranged in six rows, which extend as well defined bands from the dorsal posterior edge of the retina anteriorly over its rounded distal end, and posteriorly over its ventral surface to its ventral posterior edge. This band thus occupies both dorsally and ventrally the median portion

[1] Judging from the figures as well as the statements made by the authors quoted, the hexagonal arrangement is characteristic of the ommatidia in the following Crustaceans (exclusive of the Decapods): *Branchipus* (Burmeister, '35, p. 531, Spangenberg, '75, p. 30), *Nebalia* (Claus. '89, Taf. X. Fig. 10). *Gammarus* (Sars, '67, p. 62), *Orchestia* (Frey und Leuckart, '47, p. 204), *Phronima* (Claus, '79, Taf. VI. Fig. 48), *Cymothoa* (Müller, '29, Tab III. Figs. 5, 6, Bullar, '79, p 514), *Lygidium* (Lereboullet, '43, p. 107, Planche 4, Fig. 2[b]), *Serolis* (Owen, '43, p. 174), *Arcturus* (Beddard, '90, Plate XXXI. Fig. 4), *Anceus* (Hesse, '58, pp. 100 and 103, Dohrn, '70, Taf. VIII. Figs. 33, 34), *Squilla* (Milne-Edwards, '34, p. 117, Will, '40, p. 7, Frey und Leuckart, '47, p. 204, Leydig, '55, p. 411), and *Mysis* (Sars, '67, Planche III. Fig. 7, Grenacher, '79, Taf. X. Fig. 112). I have observed the hexagonal arrangement in the following genera: *Apus, Branchipus, Estheria, Evadne, Argulus, Gammarus, Caprella, Talorchestia, Idotea, Serolis, Porcellio, Sphæroma, Mysis,* and *Gonodactylus.*

of the retina, and separates the remaining retinal surface into two parts, one on either side of the stalk. In alcoholic specimens this median band is readily visible with the aid of a hand lens, and a little closer scrutiny shows that it is composed of six lines. These lines, of course, correspond to the six rows of ommatidia previously mentioned. The smaller ommatidia, on either side of the median band, are also arranged in lines parallel to those in the band; but, on account of their smaller size, the lines formed by them are not visible with an ordinary lens.

The smaller ommatidia in Goniodactylus are arranged upon the typical hexagonal plan (see the left half of Fig. 93, Plate VIII.). The larger ones have a somewhat similar grouping, although the fact that they are in six longitudinal rows rather obscures their hexagonal arrangement. (See the right half of Figure 93, in which three rows, and a part of a fourth, of large ommatidia are shown.) The hexagonal arrangement is not disturbed, as might be expected, on the line which separates the larger from the smaller ommatidia, but both kinds form parts in a common system. That this is true can be seen from Figure 93, where it will be observed that the *centres* of any two small ommatidia lying in the same vertical line are as far apart as the *centres* of the corresponding larger ommatidia. Moreover, as I have demonstrated by actually counting the ommatidia of long parallel series, a vertical band which contains twenty-five large ommatidia has the same length as one composed of a corresponding number of small ones. The apparent difference in numbers at first sight presented by lines of the two kinds of ommatidia is principally due to the fact that the larger ommatidia are arranged in distinct rows, whereas the smaller ommatidia are so grouped that the individuals in one row are slightly interpolated between those of the two adjoining rows (compare Fig. 93).

In Decapods the ommatidia are arranged either upon the hexagonal or tetragonal plan. In the Brachyura,[1] as well as in three families of the Macrura, the Hippidæ, Paguridæ, and Thalassinidæ,[2] the arrangement

[1] The presence of hexagonal facets has been recorded in the following genera of Brachyura: *Portunus* (Will, '40, p. 7); *Ilia* (Will, '40, p. 7, Leydig, '55, p. 411); *Cancer*; *Maja*; *Carpilius* (Frey und Leuckart, '47, p. 204); *Herbstia*, *Dorippe*, and *Lambrus* (Leydig, '55, pp. 407, 410, and 411, respectively). This form of facet is present only when the ommatidia are hexagonally arranged. Leydig ('55, p. 411) states that the outline of each facet in *Dromia Rumphii* is square, but, as his description clearly indicates, the facets are arranged upon the hexagonal plan. As my own observations show, the ommatidia in *Cardisoma Guanhumi*, Latr., *Cancer irroratus*, Say, and *Gelasimus pugilator*, Latr., are hexagonally grouped.

[2] The outline of the corneal facets is stated to be hexagonal in the following genera: *Pagurus* (Swammerdam, '52, p. 88, Cavolini, '92, p. 130, Milne-Edwards,

of the ommatidia is invariably hexagonal. In the remaining macrurous Decapods[1] the ommatidia are grouped on the tetragonal plan. This last statement, however, is not without exceptions, for in Typton, and at times also in Galathea,[2] the hexagonal arrangement appears to prevail. An explanation of these exceptions will be offered in a subsequent paragraph.

Before attempting this explanation, however, it will be well to gain a precise idea of the relation of the hexagonal and tetragonal methods of arrangement. At first sight, it might appear that these two methods had no definite relations, and were simply characteristic of different Decapods. Such, however, is not the case; for, as the development of the lobster shows, the ommatidia in a *single* animal can be arranged at first according to one plan, and afterward according to the other. In the lobster the hexagonal arrangement characterizes the earlier stages of development, and is replaced only subsequently by the tetragonal grouping. A similar change also occurs in the spiny lobster. Thus, in Phyllosoma, the larva of either Palinurus or Scyllarus, the hexagonal facets observed by Milne-Edwards ('34, p. 115) afford unquestionable evidence of the hexagonal arrangement at this stage. In the adult condition, however, both of Palinurus and of Scyllarus, according to my own observations, the ommatidia are tetragonally grouped. In the common lobster and the spiny lobster, then, the hexagonal arrangement of the early stages is replaced by the tetragonal one in the adult. These ob-

'34, p. 117, Will, '40, p. 7, Frey und Leuckart, '47, p. 204, Chatin, '78, p. 8); *Callianassa;* and *Gebbia* (Milne-Edwards, '34, p. 117). In *Pagurus longicarpus*, Say, and *Hippa talpoida*, Say, I have observed a hexagonal arrangement of the ommatidia.

[1] Judging from the figures given by various authors, the ommatidia of the following genera are characterized by the tetragonal arrangement: *Galathea* (Will, '40, Fig. III. c.); *Astacus* (Müller, '26, Tab. VII. Fig. 13, Leydig, '57, p. 252, Fig. 134, Reichenbach, '86, Taf. XIV. Fig. 226, Huxley, '57, p. 353); *Homarus* (Newton, '73, Plate XVI. Fig. 3, Parker, '90[a], p. 8); *Palæmon* (Grenacher, '79, Taf. XI Fig. 118 A, Patten, '86, Plate 31, Fig. 115); *Penæus* (Patten, '86, Plate 31, Fig. 75). As my present observations have shown, the tetragonal arrangement is characteristic of the ommatidia in *Palinurus Argus*, Gray, *Cambarus Bartoni*, and *Palæmonetes vulgaris*, Say.

[2] According to Chatin ('78, p 13) the outline of the facet in *Typton* is hexagonal. Presumably the arrangement of the ommatidia in this genus is upon the hexagonal plan. In *Galathea*, according to the figures given by Patten ('86, Plate 31, Fig. 116), the ommatidia are hexagonally arranged, although it must be borne in mind that Will's ('40, Fig. III c.) figure of the facets in *Galathea strigosa* affords unmistakable evidence of a tetragonal arrangement.

servations appear to me to afford considerable evidence in favor of the view that the hexagonal arrangement is phylogenetically more primitive than the tetragonal.

Granting this conclusion, a number of otherwise exceptional observations can be explained. Thus, as long ago as 1840, Will ('40, p. 7) called attention to the fact that in Astacus, where the ommatidia are normally arranged upon the tetragonal plan, facets near the edge of the retina are often irregularly hexagonal. The edge of the retina is well known to be the last part produced, and therefore it is probably the part least differentiated. Admitting the hexagonal arrangement to be a primitive one, it is only natural to expect that, if it persists at all, it will persist in the less modified portion of the retina. Hexagonal facets also occur on the periphery of the retina in Homarus, and are to be explained, I believe, in the same way.

On the assumption that the hexagonal plan is primitive, the occurrence of a few genera with ommatidia hexagonally arranged, in a group in which the tetragonal arrangement is the rule, can also be explained. In Typton, for instance, the hexagonal plan obtains, although in almost all Crustaceans closely related to it the tetragonal system prevails. This condition may be explained, however, by the fact that the eyes in Typton show evident signs of degeneracy, due in all probability to the parasitic habits of the Crustacean. If the hexagonal arrangement represents an early ontogenetic phase in the development of Decapods related to Typton, it would be natural to expect that in Typton itself, where the normal development of the eyes is interrupted by parasitism, this arrangement would persist permanently.

In Galathea, as I have already mentioned in a note on page 63, the ommatidia according to Will are arranged tetragonally; according to Patten, hexagonally. At first sight these observations might appear to be irreconcilable, but such is not necessarily the case. So far as I have been able to ascertain, Patten does not mention the name of the species which he studied. Possibly he may have examined some other than G. strigosa, the one from which Will's figures were drawn. In such an event, a difference in the arrangement of the ommatidia may have been characteristic of the two species, although, if both possessed well developed eyes, this difference would be somewhat anomalous. If this is not the true explanation, it is still possible that the specimens studied by Patten were somewhat immature, in which case the hexagonal arrangement might very naturally be present. From what has been said, I think it must be evident that the apparent contradiction in Will's and

Patten's statements is not so serious as might at first be supposed, and that, admitting the relations already mentioned between the two plans of arrangement, the observations of these two writers can be explained without supposing either of them to be wrong.

The probable method of rearrangement by which the hexagonal plan is converted into the tetragonal has been suggested in a previous paper (Parker, '90[a], p. 50). It involves two changes: the conversion of the hexagonal outline of the ommatidium, as seen in the corneal facet, into a square one, and the slipping of the rows of ommatidia one on the other, so that the lines which bound the four sides of each facet finally form parts of two series of lines which cross each other at right angles.

A condition somewhat intermediate between the hexagonal and tetragonal arrangement is shown in the retina of Crangon (Plate X. Fig. 123). In this genus the outlines of the ommatidia as seen in the facets are square, although their arrangement suggests the hexagonal type. The permanent grouping of the ommatidia in Crangon represents a stage slightly in advance of the condition seen in some young lobsters (compare Parker, '90[a], Plate IV. Fig. 55), and the particular features in which this advance is shown are two. First, the distal retinular nuclei in Crangon (Fig. 123) are grouped in pairs, more as they are in adult lobsters, and not in circles of six, as in young ones (compare Parker, '90[a], Figs. 5 and 55). Secondly, the arrangement of the ommatidial centres in reference to the hexagonal plan is more symmetrical in the young lobster than in Crangon, where the rows of ommatidia have apparently slipped somewhat upon one another so as to resemble more nearly the condition in the adult lobster.

I have been unable to determine with certainty what occasions the change from the hexagonal to the tetragonal arrangement. Apparently it accompanies an excessive growth on the part of the individual ommatidia. In the lobster, for instance, the ommatidia rearrange themselves between the times when the young animal is one inch and eight inches long. During this period the ommatidia increase about ten times in length and about five times in breadth. The increase is especially noticeable at their distal ends, and particularly in the cone cells. In young lobsters of one inch in length (Parker, '90[a], Plate IV. Fig. 55), the space between the cones of adjoining ommatidia is considerable; in adults, it is proportionally very much less (compare Parker, '90[a], Plate I. Fig. 5), and the cones are crowded against one another. Under these conditions, the hexagonal arrangement apparently gives way to the tetragonal. So far as I am aware, the tetragonal arrangement occurs only

in connection with this crowding of the cones, a condition found for the most part only in macrurous Decapods.

In accounting for the rearrangement of the ommatidia, the eyes in the Stomatopod Gonodactylus afford some important evidence. As I have previously mentioned, the ommatidia in this genus are of two sizes. The larger ones have several of the peculiarities characterizing the tetragonal arrangement: their facets are generally square; they are arranged in single lines, and these lines, so far as the relations of the individual ommatidia are concerned, show evidences of having slipped upon one another. The smaller ommatidia have hexagonal facets, and are clearly arranged according to the hexagonal plan. The larger ommatidia are rather closely packed; the smaller ones are arranged with more open space between them (compare Plate VIII. Fig. 93). In this genus, then, as in the lobster, the tetragonal arrangement occurs in connection with the crowding of the ommatidia.

How an increase in size, accompanied by a crowding of the retinal elements, can induce the change in arrangement which seems to follow it, I am at a loss to explain. Nevertheless, the two phenomena appear to be in some way connected.

From the preceding discussion concerning the arrangement of the ommatidia, the following conclusions can be drawn. The ommatidia, when numerous enough, present one of two plans of arrangement, the hexagonal or the tetragonal. The hexagonal plan is phylogenetically the older, and is characteristic of the eyes of all Crustaceans except some families of the macrurous Decapods, especially the Galatheidæ, Palinuridæ, Astacidæ, and Caridide. In these the hexagonal arrangement is usually replaced by the tetragonal; but in the adults of some species, especially those in which the eyes are partially rudimentary, the hexagonal arrangement persists. The change from the hexagonal to the tetragonal arrangement is connected apparently with an increase in size, and consequent crowding, of the ommatidia.

The Structure of the Ommatidia.

Each ommatidium, as I have previously mentioned, consists of a cluster of cells more or less regularly arranged about a central axis. The greatest number of kinds of cells which an ommatidium is known to contain is five. These are the cells of the corneal hypodermis, the cone cells, the proximal and distal retinular cells, and the accessory cells.

The cells of the corneal hypodermis are usually arranged in a very thin layer, and constitute the most superficial tissue in the retina. They either present no definite arrangement, as in Amphipods, or they are regularly grouped in pairs, one pair for each ommatidium, as in the majority of Crustaceans. On their external faces they produce the corneal cuticula. This is unfacetted in those Crustaceans in which the corneal cells are not regularly arranged and facetted when they are grouped in pairs.

The cone cells in each ommatidium are united to form the cone, a transparent body which extends from the corneal hypodermis proximally through the ommatidium at least as far as the rhabdome. The cone occupies the axis of the distal portion of the ommatidium.

The proximal retinular cells are usually limited to the proximal portion of the ommatidium. They are definitely arranged around the axial structure of that region, the rhabdome, and together with it form a single body, the retinula. The optic nerve fibres terminate in the proximal retinular cells.

The distal retinular cells are present in only the more differentiated ommatidia. They are two in number, and invest the sides of the cone distal to the plane at which this structure emerges from the retinula. When distal cells are present, the remaining cells of the retinula will be distinguished as proximal cells; when the distal cells are wanting, the other cells will be called simply retinular cells.

The accessory cells fill the space between the elements of an ommatidium, or between separate ommatidia. Their number is apparently inconstant, and they present a variety of forms. They may or may not contain pigment. Depending upon their source, two kinds can be distinguished, ectodermic and mesodermic.

In describing the ommatidia, I shall consider them according to the groups of Crustaceans in which they occur. Under each group the elements comprising the ommatidium will be described in the order in which they have just been mentioned.

My object in the following account is to determine, as far as possible, what the different kinds of ommatidial types are, and to define these types by a brief statement of the number and kinds of cells which characterize them.

Compound eyes are known to occur in some Ostracods, and in the larvæ of some Cirripeds, but their histological structure, I believe, has never been studied. I am therefore compelled to dismiss these two groups without further comment, and proceed with the description of

the ommatidia in other Crustaceans. The order in which the groups will be considered is one which is intended to emphasize their relations only in so far as the structure of their ommatidia is concerned. Naturally, this order will vary somewhat from the one usually given in systematic treatises. I shall begin with the Amphipods.

Amphipoda.

Within recent years the more important types of eyes in the Amphipods have been studied with such care that the structure of their ommatidia is perhaps better known than that of any other large group of Crustaceans. My own observations do little more than confirm the accounts already published.

The species of Amphipods whose eyes I have examined are Gammarus ornatus, M. Edw., Talorchestia longicornis, Say, and an undetermined species of Caprella. Of these the specimens of Gammarus and Caprella were collected at Nahant, Mass., where I also obtained several sets of eggs representing stages in the development of the former. Examples of Talorchestia were kindly supplied me from the collections in the Museum.

The *corneal hypodermis* in Amphipods was first satisfactorily described by Claus ('79, p. 131) in his account of the eyes in Phronima. It is represented in this genus by a layer of undifferentiated cells lying between the corneal cuticula and the membrane which limits the distal ends of the cone cells. A corneal hypodermis similar to that in Phronima has likewise been described by Mayer ('82, p. 122) in Caprella and Protella, by Carrière ('85, p. 156) in Gammarus, by Claus ('87, p. 15) in the Platyscelidæ, by Della Valle ('88, p. 94) in the Ampeliscidæ, and by Watase ('90, p. 295) in Talorchestia. I have also identified this structure in Gammarus, Caprella, and Talorchestia.

In Gammarus, as Carrière ('85, p. 156, Fig. 121) has clearly shown, the corneal hypodermis at the edges of the retina is directly continuous with the general hypodermis. According to my own observations this condition is not only met with in Gammarus, but also in Caprella and Talorchestia.

In Phronima, according to Claus's figures ('79, Taf. VI. Figs. 48 and 49, *Ma Z.*), the arrangement of the cells in the corneal hypodermis bears no definite relation to the subjacent cones; the distal end of each cone presents an area which is covered by about a dozen hypodermal cells. In Gammarus I have observed (Plate I. Figs. 2 and 3) an essentially similar distribution of the hypodermal cells; as in Phronima, the

number of cells which cover the area of each cone is about twelve. A corneal hypodermis of this same character also occurs in Talorchestia, although in this instance the number of cells over a cone is only about nine.

According to Watase ('90, p. 295), in the species of Talorchestia which he studied there were only two cells in the corneal hypodermis opposite each cone, or, as he expresses it, under each facet. When compared with the results recorded in the preceding paragraph, this observation appears somewhat striking, and the more so since two, the number of cells recorded, is the usual number found under each facet in other Crustaceans. If Watase's observation be correct, the relation which would thus be established between this Amphipod and other Crustaceans would be an interesting one. The desirability of confirming Watase's observation must, therefore, be evident; but unfortunately he has not given the name of the species of Talorchestia which he studied, and I have therefore not been able to verify his statement. In the only species of this genus which I have examined, viz. T. longicornis, the arrangement of the cells in the corneal hypodermis is very different from that described by Watase.

The conclusions which I draw from the preceding account are, that in the eyes of Amphipods a corneal hypodermis is present, and the cells composing it are usually not arranged with regularity.

The peculiar bodies observed by Schmidt ('78, p. 5) in the membrane between the corneal hypodermis and the retina proper in Phronima, and considered by Claus ('79, Taf. VI. Figs. 48, 49, *B. nu.*) as nuclei, are apparently not represented in other Amphipods. Their significance is still a matter of doubt.

The *corneal cuticula* in Amphipods has been described by almost all observers as unfacetted.[1] According to Della Valle ('88, p. 94), however, in some of the Ampeliscidæ this cuticula is facetted, and Watase ('90, p. 295) has also observed facets in Talorchestia. But with these two exceptions the corneal cuticula of Amphipods has been described

[1] An unfacetted corneal cuticula has been recorded in the following genera of Amphipods: *Amphithoe* (Milne-Edwards, '34, p. 116); *Caprella* (Frey und Leuckart, '47[a], p. 103); *Cyamus* (Müller, '29, p. 58, Frey und Leuckart, '47, p. 205); *Gammarus* (Müller, '29, p. 57, Frey und Leuckart, '47, p. 205, Pagenstecher, '61, p. 31, Sars, '67, p. 61, Leydig, '78, p. 235, Grenacher, '79, p. 109); *Hyperia* (Gegenbaur, '58, p. 82, Grenacher, '79, p. 111, Carrière, '85, p. 160); *Phronima* (Pagenstecher, '61, p. 31, Schmidt, '78, p 5, Claus, '79, p. 131); *Talitrus* (Grenacher, '79, p. 109); and the *Platyscelidæ* (Claus, '87, p. 15). I have observed an unfacetted corneal cuticula in *Gammarus*, *Caprella*, and *Talorchestia longicornis*.

as smooth. The absence of facets from Amphipods is naturally accounted for by the absence of a definite arrangement among the cells of the corneal hypodermis.

In the genus Tenais, the systematic position of which is probably somewhere between the Amphipods and Isopods, the corneal cuticula is stated by Müller ('64, p. 2) to be facetted, at least in the males. According to Blanc's ('83, p. 635) more recent observations, however, it is claimed to be unfacetted.

The *cones* in Amphipods have long been known to be segmented. The number of segments of which each cone is composed has been differently stated, however, by different observers. According to Claparède ('60, p. 211), the cones in Hyperia are each composed of four segments. This also is the number given by Sars ('67, p. 61) and by Leydig ('79, p. 235) for Gammarus. Both Hyperia and Gammarus have since been carefully studied, and these observations are now known to be inaccurate. Claparède was perhaps influenced in his statement by his belief that all cones were composed of four cells. Sars was probably misled by the supposed fact that in Gammarus the cone is surrounded by four bands of pigment, which sometimes give it the appearance of being divided into four segments.

The actual number of segments in the cone of Amphipods is two. This number was first recorded by Pagenstecher ('61, p. 31) for the cones of Phronima. Pagenstecher believed, however, that the cones in this Crustacean increased in numbers by division, and that they showed no indication of being composed of two segments except when they were undergoing this process. I need scarcely add that subsequent investigations have not confirmed Pagenstecher's belief. Cones composed of two segments have been observed in some six or seven genera of Amphipods.[1]

The *retinula* in Amphipods is stated by different observers to consist of either four or five cells. Five have been seen by Grenacher ('74, p. 653) and Carrière (85, p. 160) in Hyperia; by Grenacher ('79, p. 112), Claus ('79, Taf. VIII. Fig. 65), and Carrière ('85, p. 164) in Phronima; and by Mayer ('82, p. 122) in Caprella.

In Gammarus, Sars ('67, p. 61) observed that the cone had four

[1] In *Caprella* (Mayer, '82, p. 122), in *Gammarus* (Grenacher, '79, p. 110, Carrière, '85, p. 156), in *Hyperia* (Grenacher, 74, p. 652), in *Oxycephalus* (Claus, '71, p. 151), in *Phronima* (Schmidt, '78, p. 5, Grenacher, '79, p. 112, Claus, '79, p. 130), in *Talorchestia* (Watase, '90, p 296), and in the *Platyscelidæ* (Claus, '87, p. 15). In *Gammarus ornatus*, *Talorchestia longicornis*, and *Caprella*, each cone is composed of two cells.

longitudinal bands of pigment on it. Grenacher ('79, p. 110) took this as an indication that there were at least four retinular cells in the ommatidium of this genus, but he was unable to satisfy himself as to whether there were a greater number or not. Carrière ('85, pp. 156, 157) easily identified the four cells first seen by Sars, and in favorable cases observed what he thought might be indications of a fifth cell. In Gammarus ornatus, as the present observations show, the retinula is certainly always composed of five cells, one of which, as Carrière observed, is usually much smaller than the other four (compare *cl. rtn.*', Figs. 4–7).

In Talorchestia, according to Watase ('90, p. 296), the retinula is composed of only four cells. I have studied T. longicornis with the purpose of determining the number of retinular cells, and I find that, although there are four large retinular cells, there is also one small one, which is even more reduced than in Gammarus. Hence I conclude that the total number of retinular cells in an ommatidium of Talorchestia is five, not four.

Claus's statement ('71, p. 151), that in Oxycephalus the retinula is usually composed of four cells, is probably inaccurate, as Grenacher ('79, p. 114) suggests; and the same is perhaps true of Della Valle's ('88, p. 94) observation, that in the Ampeliscidæ the retinulæ contain only four cells each. It is therefore probable that the retinula in all Amphipods is composed of five cells, although possibly in some exceptional cases the number may be four.

The retinular cells in Gammarus envelop the sides of the cone, as Carrière suspected, and extend distally as far as the corneal hypodermis (Plate I. Fig. 2). In Hyperia and Phronima, according to the description and figures given by Carrière ('85, p. 161, and Fig. 128, p. 165), these cells appear to be limited to the proximal part of the retina.

The *rhabdome* in Amphipods, first described by Pagenstecher ('61, p. 30) as the cylindrical element in the eye of Phronima, presents a very simple structure. In Hyperia, according to Grenacher ('77, p. 31), it is a simple rod-like body, composed of five rhabdomeres, one for each retinular cell. In Phronima, as Claus ('79, p. 128) has shown, the rhabdome is a tubular structure with five sides. Each side of the tube, as can be seen in the figure given by Carrière ('85, p. 165, Fig. 128), corresponds to a rhabdomere. In Gammarus locusta, Grenacher ('77, p. 111) has shown that, in transverse section, the distal end of the rhabdome is cross-shaped. In G. pulex, according to Carrière ('85, p. 157), the distal end of the rhabdome in section shows four rays, the

proximal five. In Carrière's opinion, these rays indicate the five rhabdomeres. In Gammarus ornatus, the species which I have studied, the rhabdome (Plate I. Fig. 6, *rhb.*) is cross-shaped in transverse section throughout its length. Each rhabdomere has the form of an elongated plate, which is folded on its longest axis, so that its halves are at right angles to each other. In the rhabdome, the four rhabdomeres lie so that their folded edges occupy the axis of the ommatidium. Each of the four large retinular cells rests in the furrow produced by the folding of a rhabdomere (compare Fig. 6). The fifth retinular cell always lies at the end of one arm of the cross-shaped rhabdome. The two rhabdomeric constituents of that arm usually separate slightly, so as to allow the small retinular cell to slip in between them. Possibly this cell produces a small rhabdomere, as the corresponding cell in G. pulex does; but if such is the case, the rhabdomere must be a very small one, for I have not been able to discover it. A rhabdome of essentially this structure occurs in Talorchestia.

As the preceding account shows, the rhabdome in Amphipods always presents some indication of the number of rhabdomeres of which it is composed. This number is usually five, although it is possible that in Gammarus it may be only four.

In addition to the cells which have thus far been described as entering into the composition of the retina in Amphipods, certain other cells may be present. These may be embraced under the one head of *accessory pigment cells.*

In Gammarus, as Carrière ('85, p. 159) has shown, the space between the ommatidia is filled with rather large cells, the nuclei of which are usually visible with ease (Fig. 2, *nl. h'drm.*). These cells extend from the basement membrane very nearly, if not quite, to the corneal hypodermis. In the fresh condition they contain a whitish opaque pigment. On account of their having no definite arrangement, it is difficult to estimate their number, but there are probably two or three for each ommatidium. Cells similar in position to these have been described by Watase ('90, p. 296) in Talorchestia.

In Hyperia there are apparently three kinds of accessory pigment cells. One kind occurs in the region of the basement membrane (Carrière, '85, p. 161, Fig. 124, *m.*); another kind surrounds the proximal portion of the cones (Carrière, '85, p. 161); a third kind is applied to the retinulæ, and, according to Carrière, exactly equals in number the cells of the retinula itself. Possibly the cells which Grenacher ('79, p. 112) described as lying at the distal end of the retinula in Hyperia belong

to this third kind, although, as must be remembered, Grenacher states that there are only two such cells for each ommatidium.

These three kinds of accessory pigment cells, with the possible exception of those which surround the retinula, occur in the lateral eyes of Phronima (Carrière, '85, p. 164).

Almost nothing is known about the source of the accessory pigment cells in Amphipods. Those in Gammarus have no resemblance to the loose mesodermic tissue which lies in the neighborhood of the eye, and they are probably derived from the original ectodermic thickening which gave rise to the retina. Although some of the accessory pigment cells in Hyperia and Phronima have been called connective-tissue cells (Claus, '79, p. 125, Carrière, '85, p. 160), a name which might be taken to imply that they have come from a mesodermic source, nothing is really known about them which would be inconsistent with an ectodermic origin.

From the foregoing account of the ommatidia in Amphipods the following summary can be made: cells of the corneal hypodermis not definitely arranged, from about nine to twelve, — possibly two to each ommatidium; cone cells, two; retinular cells, five, — possibly in some cases four; accessory pigment cells (ectodermic?) present. Of these last there may be only one kind, as in Gammarus and Talorchestia, or there may be three kinds, as in Hyperia.

Phyllopoda.

The ommatidia in the eyes of Phyllopods present at least two structural types, one of which obtains in the Branchiopodidæ and Apusidæ, the other in the Estheridæ and Cladocera. On account of the greater convenience, the eyes in the Apusidæ and Branchiopodidæ will be considered first, then the eyes in the Estheridæ, and finally those in the Cladocera.

Branchiopodidæ and Apusidæ. — The ommatidia in these two families, and especially in the Branchiopodidæ, have been carefully studied by a number of competent investigators; their structure is consequently well known.

The material which I used in studying these eyes consisted of specimens of Branchipus, probably B. vernalis, Verrill, which I had collected in the neighborhood of Philadelphia, and which had been preserved for some time in strong alcohol. Through the kindness of Dr. W. A. Setchell, I was also able to examine a specimen of Apus lucasanus, Packard.

A *corneal hypodermis* has been described by Claus ('86, pp. 321, 322) in Branchipus and Apus. In Branchipus torticornis, according to Claus, the nuclei of the hypodermal cells are arranged around the distal end of each cone in circles of six; each nucleus participates in three circles, so that there are in reality only twice as many hypodermal cells as there are ommatidia. The corneal hypodermis in the eye of Branchipus vernalis (Plate IV. Fig. 30, *nl. h'drm.*) is similar to that described by Claus in B. torticornis. According to Patten ('86, p. 645), a corneal hypodermis is present in Branchipus Grubii, but the cells, instead of being regularly placed, as in either Branchipus torticornis or B. vernalis, are stated to be indefinitely arranged.

The *corneal cuticula* in Apus is described as unfacetted by Müller ('29, p. 56). Burmeister ('35, p. 533), Zaddach ('41, p. 46), and Frey und Leuckart ('47, p. 205). In Branchipus stagnalis the cuticula is smooth according to Spangenberg ('75, p. 30), marked by concavo-convex facets according to Grenacher ('79, p. 114), and smooth externally but facetted internally according to Leydig ('51, p. 295). This difference of opinion is probably due to the fact that in this species the facets are so poorly developed that their form can be determined only with difficulty. In Branchipus vernalis, although the corneal cuticula is facetted, the facet is not thickened in its centre, but has the form of a simple concavo-convex elevation, as described by Grenacher in B. stagnalis. In Branchipus paludosus according to Burmeister ('35, p. 531), in B. torticornis according to Claus ('86, p. 320), and in B. Grubii according to Patten ('86, p. 645), the corneal cuticula is unfacetted.

The *cone* in Branchipus, as Spangenberg ('75, p. 30) first demonstrated, is composed of four segments. This observation has since been confirmed by Grenacher ('79, p. 115), Claus ('86, p. 320), and Patten ('86, p. 645). In Branchipus vernalis (Fig. 31, *con.*) the cone, according to my observation, consists of four segments. The cellular nature of each segment was first clearly stated by Grenacher. Each cone in Apus, according to both Grenacher ('79, p. 115) and Claus ('86, p. 321), is composed of four cells.

The *retinula* in both Apus and Branchipus consists of five cells. This number has been seen in both genera by Grenacher ('74, p. 653) and by Claus ('86, p. 319). Spangenberg, however, ('75, p. 31) counted *four* nuclei in the retinula of Branchipus. Since these unquestionably represent the nuclei of the retinular cells, and since these cells are usually five in number, Spangenberg's enumeration is probably inaccurate. Pos-

sibly he was influenced when counting the nuclei by his belief that the number four was characteristic of many structures in the ommatidium. In Branchipus vernalis (Plate IV. Fig. 32, *cl. rtn.'*) the retinula contains five cells.

The *rhabdome* in Apus is short; in Branchipus (Fig. 30, *rhb.*) it is relatively long. In transverse section (Fig. 32, *rhb.*) it is circular, or at times squarish, but never pentagonal, as might be expected from the fact that it is surrounded by *five* retinular cells.

The retina in B. vernalis contains no other cells than the three kinds already described. According to Claus ('86, p. 319), blood corpuscles may make their way into the base of the retina of B. torticornis.

From the preceding account, the number of cells in the ommatidia of the Branchiopodidæ and Apusidæ can be stated as follows: cells of the corneal hypodermis, usually two, possibly variable in number in some species; cone cells, four; retinular cells, five. In Branchipus torticornis the interommatidial space may contain blood corpuscles.

Estheridæ. — The species which I studied as a representative of this family was Limnadia Agassizii, Packard. This species can usually be obtained in great abundance during summer in small fresh-water pools in the neighborhood of Wood's Holl, Mass., where my material was kindly collected for me by Mr. W. M. Woodworth.

The external surface of the retina in Limnadia, as I have mentioned in my account of the general structure of the eye in this genus, is covered with an extremely delicate corneal cuticula. This cuticula does not show the least trace of facets.

Immediately below the corneal cuticula are numbers of small nuclei (Plate IV. Fig. 37, *nl. crn.*). These, from their position, are probably to be regarded as the nuclei of the corneal hypodermis. They are not regularly arranged, and, although they sometimes lie between the cuticula and the distal end of a cone, they more frequently occur next to the cuticula in the spaces between the cones.

As a rule, each *cone* in Limnadia is composed of *five* cells (Plate IV. Figs. 37 and 38). In this respect it resembles the cones in Estheria californica and E. tetracera described by Lenz ('77, p. 30). In Limnadia Agassizii, however, cones composed of *four* cells are not infrequently met with (compare Figs. 37 and 38). Grube's ('65, p. 208) observation that the cone in Estheria is composed of two segments is probably erroneous, but Claus's ('72, p. 360) statement that in Limnadia the cone consists of four segments may be accurate, contrary to the opinion of Lenz.

The *retinular cells* in Limnadia cover the greater part of the sides of the cones, and completely hide the rhabdome (Plate IV. Fig. 36). Their number can be determined in transverse sections in the region of the rhabdome. In such sections each rhabdome is surrounded by five retinular cells (Fig. 39, *cl. rtn.*[1]). Occasionally nuclei can be distinguished in the pigment about the base of the cone. These are probably the nuclei of the retinular cells.

Besides the elements thus far enumerated, the retina in the Estheridæ is not known to contain other kinds of cells. The cells in the ommatidia of this family are, therefore, as follows: cells of the corneal hypodermis, not regularly arranged; cone cells, usually five, sometimes four; retinular cells, five.

Cladocera. — The extreme minuteness of the ommatidia in the eyes of the Cladocera renders their study especially difficult. In an undetermined species of Evadne which I have studied, the ommatidia are comparatively large, and in this respect are especially favorable for investigation. In the particular specimens which I used, however, I was entirely unsuccessful in all attempts to differentiate the nuclei. Although I tried a number of dyes and reagents, I was never able to make these structures visible. In consequence of this, there are several important questions concerning the eyes in the Cladocera which I have not been able to answer.

It is reasonable to believe that a corneal hypodermis much like that in Limnadia is present in Evadne, but, probably on account of my inability to stain the nuclei, I have seen no traces of it.

The *cones* in Evadne are very clearly composed of five segments (Plate IV. Figs. 41, 42). At their distal ends the cone cells are expanded so that their peripheral membranes (Fig. 41, *mb. pi'ph.*) are in contact with one another. At this level, however, the substance of the cone proper is collected about the axis of the ommatidium. Proximally the peripheral membranes of each cone contract, and under these circumstances the cavity of each cone cell is apparently filled completely with the differentiated material of the cone itself (Fig. 42).

A cone composed of five segments has been observed in a considerable number of Cladocera. Thus it is known to occur in Bythotrephys (Leydig, '60, p. 245, Claus, '77, p. 144), Daphnia (Spangenberg, '76, p. 522, Grenacher, '79, p. 117), Polyphemus, Evadne (Claus, '77, p. 144), Podon (Grenacher, '79, p. 117), and Leptodora (Carrière, '84, p. 678). Weismann's assertion ('74, p. 364) that the cone in Leptodora is composed of four segments is disproved by Carrière's later observations, and

Claus's statement ('76, p. 372) that the same number of segments occurs in the cone of Sida is probably erroneous. There is, therefore, reason to believe that the cones in the Cladocera are always composed of five segments.

The composition of the *retinula* in Cladocera, so far as I am aware, has never been fully worked out. In Evadne, on account of the relatively large size of the ommatidia, the number of cells in the retinula can be determined. At the proximal end of the cone, this structure is surrounded by *four* distinct masses (Fig. 43). The regularity with which these masses occur leaves no doubt as to their number. Each one probably represents a retinular cell. In transverse sections made through the rhabdome (Plate IV. Fig. 45), this structure is surrounded by *five* bodies, each one of which I take to be a retinular cell. It is therefore probable that the retinula of Evadne is composed of five cells, four of which approach nearer the surface of the eye than the fifth.

In Evadne I have seen no evidence of the existence of other cells than those belonging to the cone and retinula. According to Carrière ('84, p. 678), the interommatidial space in Leptodora contains a number of cells which envelop the cones more or less completely. These are probably to be regarded as accessory pigment cells.

From the foregoing account the following general statement can be made for the ommatidia in the Cladocera: corneal hypodermis, not observed; cone cells, five; retinular cells, five (in Evadne); accessory pigment cells present (in Leptodora).

Copepoda.

I have studied the lateral eyes in Pontella and Argulus, as representatives of the Copepods. As is well known, the eyes in these two genera differ greatly in structure, and I shall therefore describe them separately, beginning with the eyes in Pontella.

Eucopepoda. — The species of Pontella which I studied was extremely abundant at Newport in August, 1890. This animal was so transparent when living, that the general structure of its eyes could be ascertained by a simple microscopic inspection of it. In addition to its median eye, which occupies a ventral position, it possesses a pair of lateral eyes (compare Claus, '63, Taf. III. Fig. 5) situated one on either side of the sagittal plane at the antero-dorsal angle of the head.

Each lateral eye in Pontella, as Claus ('63, p. 47) has already stated, is provided with a spherical lens (Plate II. Fig. 18, *lns.*), which is usually firmly attached to the superficial cuticula. Immediately behind

this lens, and in fact covering much of its proximal face, is a rather irregular mass of cells, the retina. In the living animal the cells of the retina contain a great quantity of black or reddish black pigment. This coloring matter, however, is so readily soluble in alcohol, that in specimens preserved in that fluid all traces of it disappear. The optic nerve (*n. opt.*, Fig. 18), an imperfectly defined bundle of fibres, emerges from the retina near its posterior dorsal edge, and passes directly backward to the brain.

The lenses of the two lateral eyes in Pontella are so near each other that their median faces are almost in contact (compare Plate III. Fig. 29). The retinas of the two eyes, as Claus ('63, p. 47) has observed, are united with one another on their median faces, and so intimately that they are apparently incapable of independent motion.

The two retinas together may be rotated on their lenses through an angle of about forty-five degrees. The plane of this rotation corresponds to the sagittal plane of the body, and the rotation is accomplished by two pairs of muscles, one for each retina (compare Claus, '63, Taf. III. Fig. 6). One pair of these muscles is shown in Figure 18. They occupy a plane approximately parallel to the sagittal plane of the body, and the effects of their contractions must be apparent from their positions. When both muscles are relaxed, the retina occupies a position substantially as shown in Figure 18. By the contraction of the posterior muscle, the retina may be drawn upward and backward over the surface of the lens, till its axis, instead of pointing dorsally, is directed forward and upward at an angle of about forty-five degrees with its original position. The retina is not usually held for any great length of time in this position, but is soon returned by the contraction of the anterior muscle to its normal place. The backward motion of the retina is accomplished with such rapidity that the animal has the appearance of winking. The forward motion is rather slower.

Each lens in Pontella is composed of concentric laminæ (Plate III. Fig. 29, *lns.*). A considerable portion of its distal surface is intimately connected with the superficial cuticula (Plate II. Fig. 18), although a line of demarcation between lens and cuticula can always be distinguished.

When the anterior half of the body of Pontella is boiled in a strong aqueous solution of potassic hydrate, and afterwards subjected to the action of concentrated nitric acid, all the soft parts are dissolved, and only the very resistant chitinous structures remain. In specimens treated in this way, the lenses retain their firm connection with the superficial cuticula, and differ in appearance from those in the living ani-

mals only in that their concentric lamellæ are somewhat more distinct. The fact that the lens is composed of concentric layers indicates that it is secreted, and the resistance which it offers to reagents is weighty evidence in favor of its chitinous nature. In my opinion, therefore, the lens in Pontella is a chitinous secretion.

The development of the lens in Pontella is rather peculiar. Apparently a new lens is formed with each moulting of the general cuticula; at least, in a rather large proportion of the number of individuals examined, the lenses were abnormally small, having a diameter of one third or even one fourth of that shown in Figure 18. Moreover, in all such individuals the superficial cuticula was correspondingly thin and delicate, and when the animal was subjected to boiling potash, the segments of its body and appendages separated with a readiness never observed in specimens with large lenses. There can be no doubt, I believe, that the small lenses are always accompanied by thin cuticula, a relation which is to be explained by the immature condition of both structures.

The smaller lenses differ from the larger ones in only one important particular besides that of size. They are not in contact with the superficial cuticula. This relation can be determined better in optical sections than in actual ones, for in the latter the position of the lens is usually somewhat changed by the resistance which it offers to the knife. The centre of the small lens occupies a position relatively the same as that of the large lens, the space between the surface of the small lens and the external cuticula being filled with a cellular mass. This mass, as seen in optical sections, apparently envelops the lens on all sides, and is undoubtedly composed of the cells which secrete that structure. As the lens increases in size, the cells are probably excluded from the region between it and the cuticula, and as they retreat cement the lens to the cuticula. Upon the completion of the lens, the cells which have shared in producing it probably withdraw slightly from it to form the hypodermal thickenings which occur beneath the adjoining cuticula (Plate II. Fig. 18, and Plate III. Fig. 29, *h'drm.*). These thickenings are rich in nuclei, and often have delicate strands of protoplasm stretching to the surface of the lens (Fig. 18).

I believe that these facts justify the opinion that the lenses in the lateral eyes of Pontella are composed of chitin, that they are produced unconnected with the superficial cuticula, and that they are secondarily cemented to it. Like the cuticula itself, they are products of the hypodermis, a new lens being generated in all probability with each new formation of cuticula.

Lenses similar in position to those in Pontella have been identified in the lateral eyes of several other genera of Copepods. Gegenbaur ('58, p. 71) described such lenses in Sapphirina, and Leuckart ('59, p. 250) observed similar ones in the lateral eyes of Corycæus and Copilia. In all these genera the lenses, although biconvex, are not spherical, as in Pontella. Gegenbaur ('58, p. 71), following Leydig's generalization, believed that in Sapphirina the lenses were thickenings in the cuticular covering of the body, and Claus ('59, p. 271) considered them morphologically equivalent to a single corneal facet. Leuckart ('59, p. 250), without definitely committing himself as to the nature of the lens, states that in Copilia and Corycæus the lens is implanted in the superficial cuticula, and further describes it in Corycæus as composed of two parts, an outer and an inner. According to Grenacher ('79, p. 67), both parts can be identified in the lens of Copilia; the outer part is a portion of the superficial cuticula; the inner part, both in its optical properties and its behavior toward reagents, is unlike the cuticula. The inner part, however, contains no traces of cells, but is composed of a homogeneous substance, probably secreted. This view of the duplicity of the lens contrasts with the older idea of its origin as a thickening in the superficial cuticula.

It is possible that the lenses in the Pontellidæ and Corycæidæ are not homologous structures, but on account of their similarity I am inclined to consider them as such. Since in Pontella both parts are derived from the cuticula, I believe that a similar origin will be demonstrated for these parts in the Corycæidæ. The differences which Grenacher has pointed out between the two parts of the lens in Copilia do not necessarily oppose this view. It is possible that the cuticular secretion which forms the proximal part of the lens may originate separately from the other cuticula, as in fact it does in Pontella; and it may also be true, although this is not supported by the condition in Pontella, that the two parts, although both secretions of the hypodermis, may differ enough in their substance to account for all the peculiarities observed by Grenacher.

The *retina* and lens in Pontella are not separated by an intervening space as in the Corycæidæ, but are in immediate contact. The retina is composed of a mass of cells, the number and arrangement of which can be seen in the figures on Plate III. These figures represent a series of consecutive sections cut in planes transverse to the axis of the eye, i. e. parallel to the horizontal plane of the animal (compare Fig. 18, Plate II.). The series is complete in that it represents all

the sections which pass through the retina. The most ventral section is shown in Figure 20, the most dorsal in Figure 29.

Immediately below the lens the central part of the retina is occupied by a roundish granular mass (Fig. 18, *con.*), which in the living animal is the only part without pigment. In transverse sections this mass is seen to consist of two bodies (*cl. con. 1*, and *cl. con. 2*, Fig. 25), which extend as far as to the lens (compare Figs. 25–27). Each body contains a nucleus (*nl. con.*, Figs. 25 and 27) and consequently represents a cell. From the position which the mass occupies, and from the fact that it contains no pigment, it represents, I believe, a cone, and the two cells of which it is composed are its two segments.

Claus ('63, p. 47) states that in Pontella each retina is provided with six or more small crystalline cones, but my own observations do not confirm this statement. The body which, on account of its position, I have described as the cone in Pontella, is probably homologous with what Dana ('50, p. 133) first described as the inner lens in Corycæus, and with what subsequent investigators have called the crystalline cones in Sapphirina (Gegenbaur, '58, p. 71) and Copilia (Leuckart, '59, p. 252). Nothing, I believe, is known of the cellular composition of the cone in these genera.

The arrangement of the elements in that portion of the retina which surrounds the cone in Pontella is not easily made out. The most conspicuous structures in this region are rod-like bodies, which probably represent rhabdomeres. Eight of these, arranged in three groups, are present in each retina. The largest group, composed of five rods, lies directly beneath the cone. The rods of this group have been numbered from one to five in the retina to the left in Figures 21, 22, and 23. Posterior to this group, in the same retina, is the sixth rod, seen in Figures 24, 25, and 26. Anterior to it are the seventh and eighth rods, seen in Figures 26, 27, 28, and 29.

The outlines of the cells to which these rods belong cannot always be distinguished ; that there is a cell for each rod is evident from the fact that near each rod there is a large nucleus. The nucleus belonging to the cell from which the eighth rod was produced is shown in Figure 28 (*nl. rtn.'*) ; those belonging to the cells from which the sixth and seventh rods arose are indicated in Figure 26 (*nl. rtn'.*), and those belonging to the cells from which the central group of five rods came are seen, four in Figure 24 and one in Figure 25 (*nl. rtn.'*).

In addition to these nuclei, which judging from their positions and number are unquestionably the nuclei of the cells to which the rhab-

domeres belong, the retina contains a number of smaller nuclei (Fig. 21, *nl. h'drm.*). These nuclei have been drawn in the figures of the various sections in which they occur, and probably represent undifferentiated cells.

To what extent the retina of Pontella can be resolved into ommatidia may be seen from the foregoing account. Evidently the two cone cells, the subjacent groups of five retinular cells, and probably some of the undifferentiated cells, are the equivalent of one ommatidium. The sixth cell, with its rod, is probably the representative of a second ommatidium, and the seventh and eighth cells are probably representatives of one, or perhaps two, more.

If this interpretation be correct, the cells in the one complete ommatidium in Pontella would be as follows: corneal hypodermis, undifferentiated; cone cells, two; retinular cells, five; undifferentiated pigment cells (ectodermic?) present.

Each retina in Sapphirina, according to Grenacher ('79, pp. 69, 70), contains one group of three rhabdomeres. These are accompanied, as in Pontella, by an equal number of large nuclei. The body designated at *y*, and perhaps some of those marked *x*, in Grenacher's figure of Sapphirina (Fig. 43), may also represent isolated rhabdomeres. In Copilia, Grenacher believes that the number of rhabdomeres in each retina is three. Possibly in this genus, as in Sapphirina, the body marked *x* by Grenacher (Taf. VI. Fig. 40) may represent an isolated rhabdomere. Grenacher's observations, when coupled with what I have seen in Pontella, show that in Copepods the number of retinal elements is open to considerable variation, and that what would correspond to the retinula in Sapphirina, and perhaps in Copilia, consists of a cluster of only three cells, instead of five, as in Pontella.

Branchiura. — The ommatidia in Argulus are rather small, and their structure is consequently imperfectly known. The specimens of this Crustacean which I studied were obtained from an aquarium in which the common Killifish, Fundulus heteroclitus, had been kept. I have not been able to determine the species to which these specimens belong.

The *corneal hypodermis* in Argulus is separated from the retina proper by a space filled with blood (Plate II. Figs. 11, 12, *cœl.*). The cells in this layer (Fig. 12, *h'drm.*), as in the corneal hypodermis of Amphipods, are not arranged in groups, but are irregularly scattered. On their distal faces they produce the corneal cuticula (Fig. 12, *cta.*), which, as Müller ('31, p. 97) observed, is without facets. Proximally they are separated from the blood space by the delicate corneal membrane (Fig. 12, *mb. crn.*).

The distal face of the retina proper in Argulus is bounded by a delicate preconal membrane (Figs. 11–13, *mb. pr'con.*) and its proximal face is limited by the basement membrane (Figs. 11–13, *mb. ba.*).

The most conspicuous objects in the retina are the *cones* (Fig. 11, *con.*), which lie with their distal ends usually somewhat below the preconal membrane (Fig. 13). Each cone, as Claus ('75, p. 256) has observed, is composed of four segments (Fig. 14). The segments correspond to cells, and although the cone itself terminates proximally before reaching the rhabdome, the cone cells form an axis free from pigment and extending from the cone to the rhabdome (compare Fig. 12). In depigmented sections the peripheral membranes of the cone cells (Fig. 13, *mb. pi'ph.*) can be distinguished as sharply marked lines which extend from the sides of the cone to the sides of the rhabdome. The intercellular membranes of the cone cells in the region between the cone and rhabdome are apparently marked by thickenings which appear in both longitudinal and transverse sections (compare Figs. 13 and 15). At the distal end of the rhabdome the four cone cells separate, and, after passing partly around the rhabdome, become lost in the adjoining tissue (Fig. 16, *cl. con.*). I have not been able to discover the nuclei of the cone cells.

It is difficult to determine the number of cells in the *retinula* of Argulus. Slightly below the proximal end of the rhabdome, the retinula is divided into five distinct pigmented masses (Fig. 17, *cl. rtn.'*). Since the rhabdome (Fig. 16, *rhb.*) is composed of five rhabdomeres, it is highly probable that the retinula consists of five cells; but I have not been able to determine with precision the outline and extent of these cells.

The nuclei which are visible in the retina of Argulus closely resemble one another. They are limited for the most part to two regions (Fig. 13), one near the level of the cones, the other near the basement membrane. Apparently there are no nuclei immediately below the preconal membrane. Those which are near the cones (Figs. 13, 14, *nl. h'drm.*), judging from their arrangement and position, probably represent interommatidial pigment cells. Those near the basement membrane (Fig. 13, *nl. rtn.'*) may be the retinular nuclei, as their position seems to indicate. For some distance proximal to the basement membrane, nuclei (Fig. 13, *nl. h'drm.'*) occur among the nerve fibres. Possibly they represent scattered cells in this region, but the strong resemblance which they have to the nuclei on the distal side of the membrane induces me to believe that they too are retinular nuclei, which, as in the Amphipods, have migrated to a position below the basement membrane.

The cells in the ommatidium of Argulus are as follows: cells of the corneal hypodermis, not arranged in definite groups; cone cells, four; retinular cells, probably five; accessory pigment cells probably present.

Isopoda.

The material which I used in studying the eyes in Isopods came from several sources. I collected specimens of Asellus and Porcellio in the neighborhood of Cambridge, and the two species of Idotea which I studied were obtained at Newport. Specimens of Serolis Schythei, Lütken, and of an undetermined species of Sphæroma, were kindly furnished me from the collections in the Museum.

The ommatidia in Isopods present two types of structure: one of these is characteristic of the eyes in a majority of the members of this group; the other, so far as is known, is represented only in the genus Serolis. These two types will be considered separately, and the one which is common to the greater number of Isopods will be described first.

The *corneal hypodermis* in the more common of these two ommatidial types was first identified by Grenacher. In Porcellio, according to this author ('79, p. 107), the proximal surface of each facet is covered with two comparatively thin cells. These are the cells of the corneal hypodermis. Belloni ('81[a], p. 98, Tav. II. Fig. 11 n.) figures similar cells in the ommatidium of Sphæroma, and Beddard ('90, p. 368) concludes justly, I believe, that, of the four nuclei found near the distal end of the cone in Arcturus, two represent cone cells and two cells in the corneal hypodermis. In Idotea irrorata I have identified two cells in the corneal hypodermis for each ommatidium. The nuclei of these cells lie very near the nuclei of the cone cells (compare *nl. con.* and *nl. crn.* in Figs. 50 and 51, Plate V.). In an ommatidium of Porcellio, Grenacher ('79, pp. 107, 108) observed that the plane which separates the two cone cells also separates the two cells in the corneal hpyodermis. In Idotea, also, both kinds of cells are separated by a single plane.

The facetted condition of the *corneal cuticula* of Isopods was observed as early as 1816 by G. R. Treviranus ('16, p. 64), in wood-lice, and subsequently in the same animals by Lereboullet ('43, p. 107, '53, p. 119). The shape of the facets in different Isopods has given rise to some difference of opinion. According to Müller ('29, p. 42), in Cymothoa each has the form of a biconvex lens. Leydig ('64[a], p. 40) states, however, that in Oniscus the facets are concavo-convex with their hollow faces innermost. In Asellus, according to the figure given by Sars ('67, Planche VIII. Fig. 14), they are plano-convex with their flat faces

innermost. These differences, although at first sight somewhat contradictory, are not matters of great importance, for it is probable that each time an Isopod sheds its cuticula and a new one is formed, the lens assumes, at successive stages of its growth, outlines which coincide very closely with those recorded by the different observers. Thus, an early stage would be represented by the concavo-convex lens described by Leydig, an intermediate stage by the plano-convex lens figured by Sars, and the final condition by the biconvex lens mentioned by Müller. Either this is the explanation of the differences, or the observations of Leydig and Sars are probably erroneous, for the results of the more recent investigations point to the conclusion that the facets in Isopods have the form of a biconvex lens. Facets of this shape have been seen by Grenacher ('77, p. 29) in Porcellio, and by Bellonci ('81[a], p. 98) in Sphæroma. According to my own observations, they also occur in Idotea, Asellus, Porcellio, and, as I shall show subsequently, in Serolis. In the four genera mentioned the inner face of each facet is distinctly convex; this is also true of the outer face in Asellus and Porcellio. In Serolis and Idotea (Plate V. Fig. 50), however, the outer face is so slightly curved that it is difficult to decide whether its curvature is that of the general corneal cuticula or one peculiar to the facet itself.

That the *cone* in Isopods is composed of two segments was first observed by Leydig ('64[a], p. 41, and '64, Taf. VI. Fig. 8) in Oniscus. According to this author, each segment is spherical. Each ommatidium, therefore, contains two spheres, and these, as Leydig's figure shows, are placed side by side immediately below the corneal facet.

It is now well known that in many Isopods, especially in the woodlice, the cone itself is nearly spherical, and its two segments would consequently be hemispheres, not spheres as figured by Leydig. How Leydig's statement of the spherical shape of the segments can be accounted for, is not apparent. Since the two spheres described by him occupy the same relative positions as the hemispherical segments of a normal cone, there is not much question in my mind that they represent these segments. Possibly their separation and spherical form may have been due to the swelling action of some reagent which Leydig may have used to make the tissue transparent. A cone composed of two segments has been observed by Sars ('67, p. 110) in Asellus, by Leydig ('78, p. 256) in Ligidium, by Grenacher ('77, p. 29) in Porcellio, by Bellonci ('81[a], p. 98) in Sphæroma, by Sye ('87, p. 23) in Jæra, and by Beddard ('90, p. 368) in Arcturus. In the three genera which I have examined, Idotea, Asellus, and Sphæroma, each cone consists of two segments.

These observations naturally lead to the conclusion that in all Isopods each cone is composed of two segments. To this general statement, however, there are two noteworthy exceptions, one recorded by Sars, the other by Beddard. Sars ('67, p. 110) has shown that, of the four ommatidia in each eye of Asellus aquaticus, three have cones composed each of two segments; in the fourth, however, the cone is divided into three parts. This observation has been confirmed by Carrière ('85, p. 155). It is important to observe that in the figure given by Sars ('67, Planche VIII. Fig. 12) the three parts of the cone are not of equal size; one is about as large as a single segment in the cones of the other three ommatidia, whereas the remaining two are each about half as large. In the eyes of the species of Asellus found about Cambridge, the ommatidia are usually twice as numerous as in the European species, A. aquaticus, and, so far as I could observe, the cones in the American species were always composed of only two segments. In Arcturus, according to the figures given by Beddard ('90, Plate XXXI. Figs. 1 and 4), cones of three segments are occasionally met with.

The cellular composition of the *retinula* in Isopods was first made out by Grenacher ('74, p. 653), who found that in Porcellio this structure consisted of seven cells. Distally these cells surround the cone; proximally they are continuous with the optic-nerve fibres. A retinula consisting of seven cells has also been demonstrated by Buller ('79, p. 513) in Cymothoa, and by Beddard ('88, p. 443) in Æga and Ligia. As Beddard ('88, Plate XXX. Fig. 13) has shown, the seven cells in the retinula of Æga pass through the basement membrane and become continuous with the nerve fibres. In Porcellio, as I have observed, the fibrous ends of the seven retinular cells not only can be identified as nerve fibres below the basement membrane, but each cell contains a well developed fibrillar axis (Plate V. Fig. 46, *ax. n.*), and I therefore conclude that in Porcellio all seven cells are functional as nervous elements.

In Idotea robusta, transverse sections of the retinula in the region where the rhabdome is thickest present the outlines of what seem to be *seven* retinular cells (Plate V. Fig. 48). In positions either distal or proximal to this, however, only *six* cells appear. These six cells pass through the basement membrane and taper into nerve fibres, and their nuclei, unlike the corresponding nuclei in other Isopods, occur in that part of the cell which is proximal to the basement membrane (Figs. 49 and 50, *nl. rtd'.*). The seventh body (Fig. 48, *cl. rud.*), in those sections in which it occurs, has in all essential respects the same appearance as any one of the adjoining six cells. It differs from these, however, in that

it is usually somewhat smaller, and I therefore conclude that it is a rudimentary cell. It does not appear to contain a nucleus; granting, however, that it is a rudimentary retinular cell, one would look for its nucleus, not in the region about the rhabdome, but in the region of the nuclei of the other retinular cells, i. e. proximal to the basement membrane. Owing to the irregularity with which the fibrous ends of the retinular cells are arranged in this region, I have not been able to identify any nucleus with this rudimentary cell. Neither have I found any fibrous projections reaching from the rudiment of the cell toward the basement membrane such as might be expected provided the nucleus and a part of the rudimentary cell persisted below the membrane. Nevertheless, I believe, for the reasons already stated, that the retinula in Idotea robusta is composed of seven cells, one of which is extremely rudimentary.

In Idotea irrorata (Plate V. Figs. 53, 55) the retinula consists of only six cells, all of which possess fibrillar axes, and are therefore probably functional as nervous structures. In one retina of the several pairs of eyes which I examined, there was a single ommatidium with *seven* functional cells (Fig. 54). With this one exception, however, I have not been able to find any trace of the seventh cell in Idotea irrorata. In Arcturus, according to Beddard ('90, p. 368), the retinula is also composed of six cells.

In Sphæroma, Bellonci ('81, p. 98, Tav. II. Fig. 12) has figured and described a retinula consisting of *five* cells. These cells alternate with five other cells, which probably represent accessory pigment cells. If Bellonci's statement is correct, it must be admitted that the number of cells in the retinulæ of Isopods may be as few as five. My own observations, however, do not confirm Bellonci's account. In the species of Sphæroma which I have studied, there are *seven* cells in the retinula, four of which are large and three small (Plate V. Fig. 58). All these cells pass through the basement membrane; all the large ones, and certainly some of the small ones, are also connected with nerve fibres.

These observations indicate that in the Isopods the retinula is composed of either six or seven cells. If Bellonci's statements prove to be correct, this structure may be composed in some cases of only five cells, but my own observations are opposed to this view.

The *rhabdome* in Isopods presents two types of structure, one of which has been well described by Grenacher ('77, p. 30) for Porcellio scaber. In this species the rhabdome is composed of seven rhabdomeres, each of which remains in connection with the retinular cell which produced it. In transverse section the rhabdome has the form of a seven-

pointed star, a ray corresponding to a rhabdomere. Each ray projects into its retinular cell, not between two cells. My own observations on Porcellio confirm Grenacher's statements. A second representative of this type of rhabdome has been described by Bellonci ('81, p. 98) for Sphæroma. Here, however, the rays, although they agree in number with the retinular cells, project *between* the cells, not into them.

The second type of rhabdome is well represented in the eye of Arcturus furcatus. In this species, according to Beddard ('90, pp. 368, 369), the distal portion of the rhabdome, although surrounded by *six* retinular cells, is bounded by *four* perpendicular sides. Each of the six cells appears from its position to contribute to the formation of the rhabdome, and yet in the greater part of this structure segments corresponding to rhabdomeres are not visible. In its proximal portion, however, the rhabdome, according to Beddard, is divided into six rhabdomeres, each of which is applied to its proper retinular cell. In Idotea robusta the rhabdome (Plate V. Fig. 48, *rhb.*) is nearly square in transverse section. So far as I have been able to discover, it does not show at its proximal end any indication of rhabdomeres.

Of these two types of rhabdome, the one in which the rhabdomeres are evident is probably more primitive than the one in which their individuality is almost, if not completely lost.

The retinas of Isopods may contain, in addition to those already mentioned, two other kinds of cells. Of these the one most frequently met with fills the space between ommatidia. Cells of this kind have been identified in Porcellio by Grenacher ('79, p. 107), and it is probable that the pigment cells described by Bellonci ('81, p. 99) as intervening between the retinular cells in Sphæroma belong to this class. I have observed interommatidial cells in Idotea; here they contain few or no pigment granules, but are easily recognized by means of their nuclei (Plate V. Fig. 54, *nl. h'drm.*).

The source of these cells is not definitely known, but there appears to be no evidence in favor of their having been derived from outside the retina. Grenacher believed that those in Porcellio are undifferentiated hypodermal cells; this interpretation probably holds good for those in Sphæroma and Idotea.

The hyaline cells, the second kind of accessory cells, have been identified by Beddard ('87, p. 235, '88, Pl. XXX. Fig. 9, *h.*) in Æga and Cirolana. Since these cells are best developed in the eyes of Serolis, a full description of their structure will be deferred until the account of the eyes in that genus is given.

The cells which characterize the ommatidia in Isopods (except Serolis) are as follows: cells of the corneal hypodermis, two; cone cells, two; retinular cells, seven, six, or possibly five. Undifferentiated hypodermal cells are sometimes present, and hyaline cells occur in a few genera.

The structural peculiarities of the *ommatidia in Serolis* were first described by Beddard ('84, pp. 339–341) about seven years ago. Recently Beddard's observations have for the most part been confirmed by Watase ('90), and it must now be admitted without question that the ommatidia in Serolis differ in several important respects from those of many other Isopods.

The material which I used in studying the eyes in this Crustacean consisted of advanced embryos and matured individuals of Serolis Schythei, Lütken. This material was collected in Patagonia by the Hassler Expedition, and was preserved in strong alcohol. Fortunately, it was in good histological condition, and sections prepared from it showed very clearly the finer structure of the eyes. My observations, as the following account will show, differ in no very important respects from those of Beddard and Watase.

Although Patten's generalization, that a *corneal hypodermis* was to be found in the compound eyes of all Crustaceans, led Beddard ('88, p. 447) to look for it in Serolis, he was not able to identify it. Watase ('90, pp. 290 and 293) was more fortunate, and succeeded in finding under each facet two cells in the corneal hypodermis. I have not been as successful as Watase was in determining the exact number of hypodermal cells in an ommatidium, but I have seen enough to convince me that such cells are present. In sections approximately tangential to the external face of the adult retina, one occasionally finds nuclei (Plate VI. Fig. 60, *nl. crn.*) between the distal ends of the cone cells and the corneal cuticula. These represent unquestionably the cells of the corneal hypodermis, and are not to be confused with the nuclei of the cone cells, which lie in a deeper plane. In making sections, the corneal cuticula splintered so irregularly that the tissue immediately below it was completely disarranged. It was therefore possible to get only irregular fragments of the tissue in this region, such as Figure 60 shows, and these fragments were always too small to admit of an accurate determination of the number of hypodermal cells under a single facet. I have also been equally unsuccessful in my attempts either to isolate these cells or to study them *in situ* on the corneal cuticula.

The eyes in the adult, owing to the thickness of the cuticula, are unfavorable for the study of the corneal hypodermis; but in embryos of

even an advanced stage, the cuticula is so thin that the hypodermis can be studied with comparative ease. An ommatidium from the eye of an advanced embryo is seen in Figure 65; the ommatidium is viewed from the side. Distal to the cone (*con.*) four nuclei can be seen; one (*nl. crn. 1*) is superficial in position, three are deep. The relation of these nuclei to the ommatidium can be satisfactorily studied in sections transverse to the axis of the ommatidium. A series of three such sections is seen in Figures 66, 67, and 68. Of these, the most distal is that shown in Figure 66. This includes only the most superficial layer of the retina, and contains two nuclei (compare *nl. crn. 1*, in Figs. 65 and 66). These nuclei, as their position clearly indicates, represent cells of the corneal hypodermis. In the plane of the section which includes the three deeper nuclei of Figure 65, four nuclei are in reality present (Fig. 67); two of these (*nl. con.*) are large, and lie directly below the superficial ones in the corneal hypodermis; two are small (*nl. crn. 2*) and lie between the ends of the deeper large nuclei. Of the deep nuclei, the two large ones (*nl. con.*) rest one above each segment of the cone; in fact, as a section in a slightly deeper plane shows (Fig. 68, *nl. con.*), these nuclei coincide so closely with the segments of the cone that they must be regarded as the nuclei of the cone cells.

It is difficult to state what nuclei in the adult correspond to the smaller of the four deep ones in the embryo. The number of these nuclei (two) in the embryo equals the number of pigment cells which Watase ('90, p. 294) has described as surrounding the cone; but that these nuclei do not belong to such cells is evident from the fact that in the embryo, the nuclei of the pigment cells can be identified in a position somewhat proximal to that in which the smaller of the four nuclei occur (compare *nl. dst.* in Figs. 65 and 69.) Possibly the cells represented by these small nuclei in the embryo become in the adult the small interommatidial pigment cells, or it may be that they retain their relatively superficial positions, and, while occupying the space between the corneal facets, perhaps produce the cuticula of that region. In the fragments of the adult retina, from immediately below the corneal cuticula, small nuclei are not unfrequently met with in the spaces between the ommatidia. These are possibly derived from the smaller deep nuclei of the embryo.

It will thus be seen that my conclusions concerning the corneal hypodermis agree in the main with those of Watase; namely, that for each ommatidium there are two cells in this layer. Besides these, however, it is possible that the hypodermis may contain an equal number of other

cells, which occupy positions immediately under the cuticula and between the ommatidia.

The facets in the *corneal cuticula* of Serolis, when viewed from the exterior, are irregularly circular in outline, often approaching a six-sided form. As I have already observed, they are arranged on the plan of the hexagonal type. The distal face of each facet is flat, or only slightly convex; the proximal face is decidedly convex. The curvatures of the two faces and the thickness of the cuticula in the facet of S. Schythei was about the same as that figured by Watase ('90, Plate XXIX. Fig. 1) for the species which he studied.

The *cone*, as Beddard ('84, p. 340) first demonstrated, and as Watase ('90, p. 290) afterwards confirmed, is composed of two nearly hemispherical segments, which correspond to the two cone cells. The protoplasmic material of each cone cell covers the curved surface of the segment to which it belongs, and contains a nucleus in its distal portion. These relations have been well shown by Watase ('90, Plate XXIX. Fig. 1).

From the condition presented even in advanced embryos (Fig. 65) it is evident that the part of the cone earliest formed, is the one which is nearest the applied faces of the two cone cells, and that from this as a centre the cone has continued to increase outwards. Although at this stage the outline of the cone itself is sharply marked (Fig. 65), the external limits of the cone cells are only approximately indicated by the distribution of the pigment granules, which have begun to form in the surrounding pigment cells.

In Serolis, as in Porcellio and Idotea, the cone cells and the cells of the corneal hypodermis are separated by the same perpendicular plane. There are some complications in the structure of the cone cells which can be discussed subsequently with greater clearness.

The *retinula* in Serolis, as Beddard ('84, p. 340) first observed, is peculiar in that it is composed of only *four* cells. My own observations add almost nothing that is new to the previous accounts of this structure. The figure which Watase has drawn ('90, Plate XXIX. Fig. 1) of the characteristic form of the retinular cell when viewed from the side and its relation to its rhabdomere, reproduces very closely the structural conditions which I have observed in S. Schythei.

The *rhabdome* in Serolis has been carefully studied by Beddard ('88, pp. 448–450). Owing to the complexity of its structure, one meets with difficulties in attempting to interpret its parts in terms of the relatively simple rhabdome of many Crustaceans. The peculiarities of this struc-

ture can be approached most satisfactorily perhaps from the side of its adult anatomy.

In a transverse section of the distal end of the rhabdome, five structures can be observed (Fig. 61). Four of these (Fig. 61, *rhb'm.*) are squarish pieces confluent on one side with a retinular cell, and in contact with one another only at their angles The sides of these pieces which are directed towards the axis of the ommatidium are convex, and together bound a central area which contains the fifth or axial structure (*cl. con.*). Each of the squarish pieces also exhibits a line slightly concave towards the axis of the ommatidium. This line, which might be taken for the separation between the axial and peripheral structures, is in reality entirely within the latter. That these are five separate structures is indicated by the fact, that in transverse section, when for any reason the elements have been broken apart, the separation almost always occurs on the lines which I have described as the limits of the different pieces.

Evidently the squarish masses (*rhb'm.*) on the axial faces of the retinular cell correspond to the rhabdomeres of other Crustaceans, and like these structures are produced by the cells to which they are attached. It is more difficult to explain the axial element, for it shows no indication of having been produced by the surrounding retinular cells, nor are there other cells in the neighborhood to which its production could be referred.

When the longitudinal extent of these structures is considered, the difficulty of explaining the axial portion is increased. In S. Schythei the rhabdomeres extend only a short distance distally and proximally, but throughout the whole of that distance they are closely applied to the axial face of the retinular cells. This condition has been well figured by Watase ('90, Plate XXIX. Fig. 1), and supports the statement already made that these bodies correspond to the rhabdomeres in other Crustaceans. I have never observed a rhabdomere, such as that figured by Beddard ('87, p. 234), in which the proximal half of the structure is not in contact with the retinular cell. The axial part has a much more considerable extent in a longitudinal direction than the rhabdomeres. Apparently it is continued proximally into a fibrous bundle which stretches towards the basement membrane, where according to Beddard ('88, p. 449) it may terminate as a single fibre.

From what has just been stated it must be evident that the so called rhabdome of Serolis consists of two sets of structures, one of which includes the four rhabdomeres and the other the axial part with its proximal fibrous prolongation.

The development of these structures has been studied by Beddard ('88, p. 450). In the youngest embryos which he examined, the axial portion was already formed, and at that stage it was closely invested by the four retinular cells and two other cells, the hyaline cells. Judging from their positions, Beddard believes that both kinds of cells may contribute to the formation of the axial structure, although the fact that this body is squarish in transverse section leads him to conclude that the four retinular cells play the more important part in its formation. Beddard regards the axial body as the rhabdome of the immature eye. In his opinion, the rhabdome in the adult is produced by subsequent secretions from the retinular cells, and presents the form of the four rhabdomeres already described. Although these rhabdomeres form the principal part of the rhabdome in the adult eye, he believes that the rhabdome of the earlier stages persists as the axial fibrous structure in the later stages, and constitutes perhaps the greater part of its distal continuation between the rhabdomeres.

Unless some such explanation of the origin of the axial part of the rhabdome as that proposed by Beddard be accepted, it is difficult to understand how the fibrous portion could arise as a secretion; for in the adult the proximal portion of it is touched by neither retinular nor hyaline cells.

Granting for the moment the adequacy of Beddard's explanation of the origin of the axial part, we are still confronted by what appears to me to be unparalleled in the structure of the eyes in Arthropods, namely, an ommatidium which produces two distinct rhabdomes. This may not be an impossibility, but if it occurs at all, it is certainly exceptional.

I believe, however, that the so called axial part of the rhabdome in Serolis is capable of another interpretation, against which the objections already suggested cannot be urged. That the axial portion terminates proximally on the basement membrane has been fairly well established by Beddard. The distal termination of it, however, has not been so clearly made out. It is my belief that the axial structure is directly continuous distally with the cone cells; in other words, that this structure is to be regarded as a proximal extension of the cone cells, not as a part of the rhabdome. The termination at the basement membrane of this prolongation of the cone cells, as observed by Beddard, is perfectly consistent with the interpretation which I have suggested, and makes the condition in Serolis similar to that in Homarus, where the fibrous ends of the cone cells also terminate on the basement membrane. That the fibrous structure should be present in the embryo of

Serolis before the formation of the rhabdome proper is rather in favor of my interpretation than opposed to it. The direct evidence that the axial body is a proximal extension of the cone cells is not as conclusive as could be desired. The condition which most favors this view is as follows. In longitudinal and transverse sections of the ommatidia, both in adult and embryonic specimens, no line of separation has been observed between the protoplasm at the deep end of the cone and the substance which occupies the axial part of the ommatidium proximal to the cone (compare Fig. 65). In attempting to determine the true relation, it is important to keep clearly in mind the fact that the proximal end of the cone, usually bounded by a sharply marked line, is *not* the proximal end of the cone cells; but; as Watase ('90, Plate XXIX. Fig. 1) has well shown, the cone is surrounded proximally as well as laterally by the protoplasmic material of its cells. It is this material, not that of the cone proper, which forms the proximal elongation.

I had hoped that by isolating the elements of the retina I could obtain more conclusive evidence of the connection of these parts, but my efforts were of no avail. My ill success was due, I believe, not to any want of connection between the structures treated, but to the fact that the material at my disposal had been kept so long in strong alcohol that it had become unfit to serve for isolation. This conclusion seems to me to be confirmed by the fact that I was unable even to isolate satisfactorily the retinulæ, structures which are usually separable with ease in the fresh retinas of most Crustaceans.

If the view which I have set forth in the foregoing paragraphs concerning the interpretation to be put upon the axial part of the so called rhabdome of Serolis be correct, it follows that the true rhabdome of this Crustacean must be considered as composed of four rhabdomeres, each of which is applied to the axial face of its appropriate retinular cell, and that these four rhabdomes are prevented from uniting with one another by a proximal extension of the cone cells which occupies the axis of the ommatidium from the cone to the basement membrane.

Beddard ('84[a], p. 21), in his account of the eye in S. Schythei, states that the cone is "enclosed in a sheath of deep black pigment cells," and Watase ('90, p. 294) has observed that in this genus there are two such cells for each ommatidium. I believe that the number has been given correctly, for although I have not satisfactorily isolated the cells, I feel confident that I have identified their nuclei, and the number of these is twice that of the ommatidia.

The nuclei of these pigment cells are most satisfactorily seen in ad-

vanced embryos (compare *nl. dst.*, in Figs. 65 and 69). In transverse sections at this stage (Fig. 69) each cone is surrounded by a circle of six nuclei. Each nucleus, however, participates in three adjoining circles, consequently there are only twice as many nuclei as ommatidia. In the adult the nuclei of these pigment cells (Fig. 60, *nl. dst.*) occupy the same relative positions as in the embryo; in the latter, however, they are usually somewhat hidden by the pigment which surrounds them.

In the embryo the nuclei of the pigment cells surrounding the cone resemble very closely, except in point of size, the nuclei of the retinular cells (compare *nl. dst.* and *nl. px.* in Fig. 65). In the nuclei of the retinular cells there is usually one distinct nucleolus, sometimes two, but as a rule no finer particles. This condition also obtains in the nuclei of the pigment cells. Not only are the nuclei of these two kinds of cells similar in the embryo, but they are also much alike in the adult (compare *nl. dst.* in Fig. 60 with *nl. rtn.'* in Fig. 63).

Because of this resemblance, I believe that the pigment cells which surround the cone can be fairly considered to be modified retinular cells, which have lost their sensory function in precisely the same way as in the case of the distal retinular cells in Decapods (see Parker, '90[a], p. 57). If this interpretation of the pigment cells be accepted, it follows that in Serolis, as in Decapods, two kinds of retinular cells are present, proximal and distal, and that the primitive ommatidium from which that of Serolis was derived probably contained six retinular cells functional as nervous structures. It need scarcely be added, that this number is characteristic for the ommatidia of many Isopods.

The retinula in the species of Sphæroma which I studied presents an appearance which suggests the differentiation of simple retinular cells into proximal and distal cells. In Sphæroma there are seven retinular cells (Plate V. Fig. 58); three of these are considerably reduced; the remaining four are large, and recall the four retinular cells of Serolis. In transverse sections it can be shown that the four large cells in Sphæroma not only resemble in appearance the four proximal cells in Serolis, but that they occupy the same relative positions in the ommatidium. In Serolis the plane which separates the two cone cells of any given cone, when extended, separates the four proximal retinular cells into two groups of two cells each (compare Plate VI. Fig. 68 with Figs. 71 and 72). The plane of separation in the cone of Sphæroma divides the retinula by passing *through* the single small retinular cell shown in the lower part of Figure 58 (Plate V.) and *between* the two small cells on the opposite side, thus separating the four large retinular cells into two groups, as in Serolis.

The change which would convert an ommatidium like that in Sphæroma into one like that in Serolis is easily imagined. It would consist in the complete abortion of one of the three small retinular cells, and the conversion of the other two into the pigment cells surrounding the cone.

In addition to the elements which have already been described in the ommatidium of Serolis, there are certain small pigment cells which occur for the most part in the region of the retinulæ. Beddard ('84[a], p. 21) describes these as long branching "connective-tissue cells," a name which might imply that they originated from the mesoderm, and were therefore intrusive. Watase ('90, p. 293, Plate XXIX. Fig. 1) has also described and figured these cells, but distinctly states his belief that they are reduced ectodermic cells. In the adult I have observed in the region of the cones, as well as near the retinulæ, certain small nuclei which are usually surrounded with more or less black pigment. These, I believe, represent the cells described by Beddard and Watase. In the embryo certain scattered nuclei (*nl. h'drm.*, Figs. 65 and 70) occur in the spaces between the ommatidia. It is probable that these nuclei are ectodermic in origin, and I am at a loss to know what has become of them in the adult, unless they form the pigment cells already mentioned. I am therefore inclined to believe, with Watase, that the small additional pigment cells are reduced ectodermic cells.

The presence of the *hyaline* cells in the ommatidium of Serolis is, as Beddard has pointed out, almost a unique feature. These cells, usually two in each ommatidium, fill the space immediately below the rhabdome. They are bladder-like (Fig. 62, *cl. hyl.*) and contain each a large granular nucleus. Although it is stated that there are usually two of these cells in each ommatidium, I never found more than one to an ommatidium in the several eyes of S. Schythei which I examined. This circumstance, however, is not surprising; for, as Beddard ('84[a], p. 22) has remarked, the number of these cells is subject to variation, there being sometimes one, sometimes two, for each ommatidium. In S. Schythei the single hyaline cell envelops more or less completely the distal part of the fibrous portion of the cone cells, so that this part seems to pierce the hyaline cell. A closer inspection, however, will usually show two lines extending from the fibre to the periphery of the hyaline cell (compare Fig. 62), and these lines indicate, I believe, the two walls of the cell which have been infolded by the presence of the fibre during the growth of the hyaline cell.

The source of the hyaline cells is not definitely known. Their nuclei (Fig. 65, *nl. hyl.*), as Beddard ('88, p. 450) has observed, are present

in the retinas of embryos; and, although the cells may possibly be intrusive, the evidence on the whole favors the view that they are ectodermic in origin.

Several functions have been attributed to the hyaline cells. Their close connection with what Beddard took to be the proximal extension of the rhabdome led him ('88, p. 450) to suspect that they might be rudimentary retinular cells, but, as he (p. 451) further remarks, the fact that no nerve fibres are connected with them opposes this view. Their transparency suggested to him ('84[a], p. 22) that they might form a part of the dioptric apparatus; but it is difficult to understand, considering their position, precisely what that function would be. I am inclined to believe, with Watase ('90, p. 293), that they are chiefly concerned with the support of the structures occupying the basal portion of the retina.

In the retina of S. Schythei many of the open spaces between the cones and the basement membrane contain free non-pigmented cells (Fig. 61, *cp. sng.*). These have a distinct nucleus, finely granular protoplasm, and a sharply marked outline. On account of the extreme variations in form which the different cells present, it is probable that when living they exhibited amœboid motion. In appearance they correspond exactly to the blood corpuscles of the body spaces, and as they occur not only in the retina, but also in the rather large openings through the basement membrane (compare Fig. 64), and in the space proximal to this membrane, I am of opinion that they are blood corpuscles.

The peculiarities which have led me to consider the ommatidium in Serolis separately from that of other Isopods, are two: the possession of one or more hyaline cells, and the presence of only four retinular cells. The latter peculiarity, as I have already shown, is not fully established; for in this genus, as in many other Isopods, the ommatidium really contains six cells, although two of these, the distal ones, are probably no longer functional as nervous structures. The other peculiarity, the possession of hyaline cells, is not a very important characteristic, for, as Beddard ('87, p. 235) has shown, these cells also occur in Æga; and it is probable, moreover, that they must be regarded as abnormally enlarged elements, specialized from among those cells which in other Isopods fill the spaces between the ommatidia. What distinguishes the ommatidium in Serolis from that of other Isopods is, therefore, not so much the possession of hyaline cells as the fact that its retinular cells are differentiated into two sets, proximal and distal.

In accordance with the facts already presented, the number of cells contained in the ommatidium of Serolis can be stated as follows: cells of the corneal hypodermis, two, with possibly two others interommatidial in position; cone cells, two; retinular cells, six, two distal and four proximal; hyaline cells, one or two; a variable number of small pigment cells of ectodermic (?) origin.

Leptostraca.

The histological structure of the ommatidia in the Nebaliæ has been investigated, so far as I am aware, only by Claus ('88, pp. 65–84). I have had no material for the study of the eyes in these Crustaceans, and I can therefore only present, in the form of a summary, the more important results of Claus's exhaustive study.

In Nebalia there is a *corneal hypodermis* (Claus, '88, pp. 68 and 69), the cells of which are grouped in pairs. As in many of the higher Crustaceans, there is one pair of these cells for each ommatidium. The *corneal cuticula* is facetted; the outlines of the facets are circular, and adjoining facets are separated from one another by a small amount of intervening cuticula (Claus, '88, Taf. X. Fig. 10). The *cones* are composed of four segments (Claus, '88, p. 69). The structure of the *retinula* is somewhat complex. The greater part of the rhabdome is surrounded by seven retinular cells. Distal to these cells, however, are seven pigment cells, which enclose the proximal prolongation of the cone cells and the distal end of the rhabdome. Such a relation between pigment cells and retinular cells is not of common occurrence among Crustaceans, and it is possible that the bodies which Claus has taken for pigment cells are really the distal ends of the retinular cells. Claus describes and figures what he believes to be the nuclei of both kinds of cells, but I think his figures fail to show that these nuclei are within the limits of the cells to which they are said to belong. It seems to me quite possible that what he has described as two circles of seven cells each may be merely one circle seen at two different levels, as the correspondence in numbers suggests. This single circle would be of course composed of retinular cells, the nuclei of which are probably the distal ones of the two sets described by Claus. The proximal nuclei, which, according to Claus, belong to the retinular cells, occupy positions not unfrequently taken by the nuclei of accessory pigment cells, and I am inclined to think that such is their real nature. This interpretation would be more in accordance with the conditions found in ommatidia which have seven retinular cells than is the one given by Claus; but as I have not

had the opportunity of studying the eyes in Nebalia, I can offer it merely by way of suggestion.

Probably two kinds of accessory cells are present in Nebalia; one of these extends from the corneal cuticula to the basement membrane, the other, the presence of which is not so fully established, probably occurs near the basement membrane.

Cumaceæ.

Excepting what is contained in Burmester's ('83, pp. 35–37) account of the degenerate eyes in Diastylis (Cuma) Rathkii, nothing, I believe, is known of the finer structure of the eyes in the Cumaceæ. The specimens at my disposal for the study of these eyes proved upon examination to be blind. At least, the optic plates of all the individuals which I examined, both when studied from the exterior and when examined in sections, showed no evidence of eyes. My material consisted of specimens of Diastylis quadrispinosa, G. O. Sars, and of three other undetermined species, two of which belonged to the genus Diastylis and one to Eudorella. These were kindly sent me by Prof. S. I. Smith.

Schizopoda.

The species of Schizopod the eyes of which I have studied is Mysis stenolepis, Smith. Specimens of this Crustacean were kindly collected for me at Wood's Holl, Mass., by Mr. C. B. Davenport. I am also under obligations to Dr. H. V. Wilson, of the United States Fish Commission, who at my request sent me specimens of this species freshly preserved in Müller's fluid.

In several of the previous accounts of the eye in Mysis the nuclei of the *corneal hypodermis*, although recognized, have been described as Semper's nuclei, i. e. as nuclei of the cone cells. The differences between the hypodermal nuclei and those of the cone cells can be easily seen in Mysis stenolepis (Plate VII. Fig. 73). In this species the hypodermal nuclei (*nl. crn.*) lie in a plane somewhat nearer the external surface of the eye than the nuclei of the cone cells (*nl. con.*). In transverse sections at the proper levels, each ommatidium will be seen to contain two elongated nuclei (Fig. 75, *nl. crn.*) belonging to the corneal hypodermis, and two oval nuclei (Fig. 76, *nl. con.*) in the cone. The hypodermal nuclei occupy such positions that the plane of separation between their cells would be at right angles to that between the cone cells (compare Figs. 75 and 76). The group of four nuclei, two belonging to the corneal

hypodermis, and two to the cone cells, correspond without much doubt to the so called four Semper's nuclei mentioned by Claparède ('60, p. 194) in Mysis flexuosa, and described by Sars ('67, p. 33) in M. oculata. Nusbaum ('87, p. 179) also observed four similar nuclei in the developing eye of Mysis chameleo, and Grenacher ('79, p. 118) described the same number in Mysis vulgaris. In the last named species, according to Grenacher, the four nuclei are grouped in two pairs, one of which occupies a more distal plane in the ommatidium than the other. The more superficial pair undoubtedly belongs to the corneal hypodermis, the deeper pair to the cone cells.

It must be evident, then, that the nuclei of the cone cells and corneal hypodermis have not always been carefully distinguished. In all cases where they have been separated, the corneal hypodermis has been shown to possess two nuclei for each ommatidium.

The *corneal cuticula* in Mysis, as Frey and Leuckart ('47[a], p. 113) first pointed out, is facetted, and the outline of the facet is a circle. In Mysis stenolepis the circumference of the facet is tangential to the circumferences of six adjoining facets (Fig. 74). In Mysis vulgaris, Grenacher ('79, p. 118) has shown that the facet is not lens-like, but is of uniform thickness throughout. In M. stenolepis, however, the cuticula is often slightly thicker at the middle of the facet than at its edges (Fig. 73, *cta.*). In this respect, therefore, different species probably vary.

The *cones* in Mysis vulgaris, according to Grenacher ('79, p. 118), are composed of two segments. The same number is also present in the cones of M. stenolepis (compare Figs. 76–78, *con.*). In longitudinal sections the cone (Fig. 73, *con.*) appears to consist of a uniformly and finely granular substance enveloped in a delicate but distinct membrane. Near the distal end of the cone the material which composes it becomes more coarsely granular; in this the nucleus of the cone cell is usually lodged. Cones (Fig. 92) which have been isolated in macerating fluids are plumper and apparently not so contracted as those which have been subjected to the process of cutting. The nuclei also are rounder and fuller. The cone proper (Fig. 92 *con.*) occupies a more central position in the cone cells, and is surrounded by a finely granular material, which is especially abundant at the proximal end. The difference between the cone proper and this granular material was not generally observable in *sections* of the cones. In all of the many cones which I succeeded in isolating, the proximal ends invariably had a broken appearance. Consequently, I believe that I have never completely isolated a pair of cone cells. The question of the proximal extent of the cone I shall recur to later.

The *retinular cells* in Mysis are of two kinds, proximal and distal. The proximal cells extend from the basement membrane distally to the level at which the cone rapidly contracts. The pigment which they contain is for the most part concentrated around the rhabdome, and their nuclei occupy a distal position in the cell (Fig. 73, *nl. px.*).

In Mysis the number of cells comprising the retinula is at least seven (Figs. 85–87). Possibly, as I have elsewhere suggested (Parker, '90[a], p. 55), the total number of cells in this retinula, as in that of Homarus, may be eight.

In order to determine this question, I have counted the number of nuclei in several retinulæ of Mysis. The enumeration of these can be easily followed in Figures 79 to 82. These figures represent successive transverse sections through four ommatidia, in the region occupied by the proximal retinular nuclei. The axis of each ommatidium is marked by the fibrous portion of the cone cells (*cl. con.*), and the same ommatidium is designated in different sections by the same Roman numeral. The nuclei in ommatidium II. can be counted the most readily. In Figure 79, which represents the most distal section of the series, the cone in ommatidium II. is surrounded by a circle of six nuclei, which have been numbered from 1 to 6. Each of these nuclei, however, participates in three circles (compare nucleus 5), and hence only two of the six can be referred to ommatidium II. Two similar circles occur, one in the sections shown in Figure 80, and one in that shown in Figure 81. As in the former instance, two nuclei in each circle belong to ommatidium II. In these three circles, then, there are in all six nuclei to be allotted to ommatidium II. In addition to these nuclei, it will be noticed that to the right of the cone in Figure 80 there is one more nucleus (No. 7), and still another in a similar position in Figure 82. These two nuclei, when added to the six already summed up for ommatidium II., make a total of eight nuclei for this ommatidium.

The same number of nuclei occurs in each of the other three ommatidia, but their arrangement is not quite so regular as in the one just counted. From this I conclude that the number of nuclei in a retinula of Mysis is eight.

The different nuclei in this retinula usually present a very uniform appearance. The most proximal one differs somewhat from the others in being more elongated (compare Figs. 73 and 82). The seven distal nuclei, on account of their general resemblance, belong, I believe, to the seven functional retinular cells. The single proximal nucleus probably represents an eighth rudimentary cell. The position of this nucleus,

proximal to the other retinular nuclei, is similar to that occupied by the nucleus of the rudimentary retinular cell in Homarus (compare Parker, '90[a], pp. 20, 21).

The *rhabdome* in Mysis stenolepis lies in the proximal portion of the retina. It is rather stout, blunt at its distal end, but sharper proximally (Fig. 90). Its surface is marked with coarse corrugations. In transverse section, its outline is a square; this is subdivided by two lines into four smaller squares, a condition already observed by Grenacher ('79, p. 119) in M. flexuosa. The relation of the retinular cells to these divisions of the rhabdome can be clearly seen in Figure 87.

According to Grenacher's account ('79, p. 118), a rod-like structure extends, in Mysis vulgaris and M. flexuosa, through the axis of the ommatidium from the distal end of the rhabdome to the region of the proximal retinular nuclei. Whether this rod be a proximal continuation of the cone, or a distal extension of the rhabdome, Grenacher found it difficult to decide. He is inclined, however, to the former opinion.

A similar structure occurs in the ommatidia of Mysis stenolepis. Although I have made repeated attempts, I have never succeeded in isolating the rod in connection with either the rhabdome or the cone cells. In transverse sections, the distal end of it appears in a position slightly proximal to the retinular nuclei (Figs. 73 and 83). The cone cells extend proximally as a transparent axis to this region, and the most distal indications of the rod are four fibres which lie on the periphery of what I take to be the proximal end of the cone cells (Fig. 83). Somewhat deeper than this, the four fibres thicken, and finally fuse (Fig. 84), producing a body which in transverse section has the outline of a four-pointed star. In a plane slightly more proximal, the outline changes to a squarish one (Fig. 85), and this is retained almost to the proximal end of the rod. Throughout its extent, this problematic rod is closely surrounded by the seven proximal retinular cells (Fig. 85). It is separated from the rhabdome by what appears to be an open space (Fig. 90, at the level of the dotted line 86). In transverse sections (Fig. 86), however, this space is seen to be divided by delicate membranes into four compartments.

These facts, however, do not aid much in deciding the relationship of the rod. The fact that it shows indications of being composed of four parts suggests its connection with the rhabdome. The four parts of which it consists do not, however, correspond in position to the segments of the rhabdome, but fall between them. (Compare Figs. 83 and 87.) On the other hand, if it were an extension of the cone, one would

expect it to be composed of two, instead of four parts. Its position, however, is one which is more frequently occupied in other Crustaceans by a slender extension of the cone cells than by a process from the rhabdome, and, notwithstanding its division into four parts, I am inclined to agree with Grenacher, and to regard it as belonging to the cone cells rather than the rhabdome.

The distal retinular cells in Mysis surround the lateral faces of the cones (Fig. 73, *cl. dst.*). Apparently they reach the cuticula; their proximal ends are attenuated and become lost in the region of the nuclei of the proximal cells. Their pigment is limited to their proximal halves, and consists of a distal layer of brownish material, proximal to which is a much more extensive deposit of blackish granules. Each cone is surrounded by six of these cells, as can be seen from their outlines (Fig. 78, *cl. dst.*), and still more satisfactorily from the arrangement of their nuclei (Fig. 75, *nl. dst.*). Each cell, however, participates in three circles; consequently, there are only twice as many of these cells as ommatidia.

The axis of each distal retinular cell is occupied by a transparent rod, which in transverse section has the appearance of a light spot (Fig. 77). In depigmented sections stained with Kleinenberg's hæmatoxylin, these rods are deeply colored (Fig. 78). I shall recur to their probable significance.

The pigment which is found in the region of the rhabdomes in Mysis is of two kinds: blackish granules, and a fine flaky material, white by reflected light, yellowish by transmitted light. The black granules are for the most part contained in the retinular cells. The lighter pigment is always associated with certain nuclei, two of which are shown in Figure 90 (*nl. ms'drm.*). These nuclei are closely invested by the pigment, and probably belong to the cells in which the pigment is contained.

The source of the yellowish pigment cells is not easily determined. Apparently they are not limited to the retina, but also occur in the spaces below it. At least these spaces contain masses of pigment and nuclei which in all essential respects are similar to those distal to the membrane (compare the two nuclei, *nl. ms'drm.*, Fig. 90). In one case the nucleus of one of these cells was found apparently caught in its passage through an opening in the basement membrane (Fig. 91). For these reasons I believe that the yellowish pigment cells on the two sides of the membrane have had the same origin. The question as to the source of the yellowish pigment cells in the retina, therefore, appears

to me to involve that of the origin of the similar cells beneath the retina. If I am right in this conclusion, all these cells must either have arisen in the retina, many of them migrating in a proximal direction out of it, or they must have had some extra-retinal origin, some of them migrating into it. On account of the considerable numbers in which they exist in the spaces below the retina, it seems to me much more probable that they have had an extra-retinal origin than that they have come from the retina itself. If this is their source, it is evident that those which are in the retina are intrusive. The nucleus which has already been mentioned as caught in an opening of the basement membrane (Fig. 91) has more the appearance of a body which is making its way into the retina than of one which is moving in the reverse direction, and may therefore be regarded as confirming to some extent the view of the extra-retinal origin of these cells. Their source, however, cannot be stated with certainty. Their power of migration implies amœboid activity, and this might be taken as an indication of their mesodermic origin.

The following cells characterize the ommatidium of Mysis: cells of the corneal hypodermis, two: cone cells, two; proximal retinular cells, eight, one of which is rudimentary; distal retinular cells, two; accessory pigment cells (mesodermic?) present.

Stomatopoda.

The material which I have had for the study of the eyes in the Stomatopods consisted of two specimens of Gonodactylus chirarga, Latr. These were kindly given me by Mr. W. S. Wadsworth, who had collected them in the Bermudas. One of them had been killed in hot water and preserved in alcohol; the other was both killed and preserved in strong alcohol; both were in excellent histological condition.

In Gonodactylus, as I have previously mentioned, there are two kinds of ommatidia; these differ in no important respect except size.

Longitudinal sections of both kinds are represented on Plate VIII.; the figure of the larger kind (Fig. 94) is taken from a depigmented section, that of the smaller one (Fig. 95) from a section containing the pigment in its natural condition. In the following description I shall give an account of the structure of the larger ommatidia, alluding to the condition of the smaller ones only when it differs in some important respect from that of the others.

The *corneal hypodermis* is represented in the ommatidium of Gonodactylus by two cells, the nuclei (Figs. 94–96, *nl. crn.*) of which can

be recognized easily. Directly under the corneal cuticula each pair of hypodermal cells is in contact with similar pairs belonging to adjoining ommatidia, so that the layer here forms a continuous sheet. In a more proximal plane the neighboring pairs of hypodermal cells are not in contact (compare Fig. 93, a tangential section in which the extreme right-hand edge represents the condition immediately below the cuticula, while the parts to the left represent central portions successively more proximal in position). The only indication of a separation between the two hypodermal cells of each pair is seen in the distal projection of the cone between the two hypodermal nuclei (compare Figs. 94 and 96, *con.*).

The *corneal cuticula* in Gonodactylus is facetted, but the proximal and distal faces of the facets are apparently plane. Over the smaller ommatidia the facets are hexagonal in outline, whereas over the larger ones they are rectangular, and their arrangement is often indicative of the tetragonal system. In Squilla mantis, according to Will ('40, p. 7), the facets are hexagonal.

The *cones* in Gonodactylus are composed for the most part of a uniformly granular substance. Distally, they are pointed and probably touch the corneal cuticula; proximally, they terminate at the rounded end of the rhabdome (Fig. 94). Each cone contains in its distal enlargement four nuclei (Fig. 97, *nl. con.*), two of which lie directly proximal to the nuclei of the corneal hypodermis, while the remaining two alternate with them (compare Figs. 96 and 97). The proximal part of the cone is divided longitudinally into four segments (Fig. 98). Each segment, if extended distally, would include one of the four nuclei, and corresponds to one of the four cells by which the cone was produced. In Squilla mantis, according to Steinlin ('68, p. 17), the cone is also composed of four segments.

The *retinular cells* of Gonodactylus are of two kinds, proximal and distal. The proximal cells, constituting the retinula itself, surround the rhabdome completely, and extend distally only a short distance beyond it (Fig. 95). They contain only a small amount of pigment, which is concentrated in two regions, at their distal ends and near the basement membrane. The rhabdome is surrounded throughout its length by a thin but rather dense layer of pigment. This layer is more extensive in the smaller ommatidia (Fig. 102) than in the larger ones. The nuclei of the proximal retinular cells (Figs. 94 and 95, *nl. px.*) are located near their distal ends.

The number of cells in the retinula of Squilla, as described by Grenacher ('77, p. 33) and by Hickson ('85, p. 341, Fig. 2), is seven. In

Gonodactylus (Fig. 101) the retinular cells are certainly as numerous as in Squilla; but seven obvious cells in the retinula, as I have already shown in Mysis, may suggest the presence of eight in all, one of them being rudimentary. This condition is in fact characteristic of Gonodactylus also, as can be seen in the series of ommatidia shown in Fig. 100. These six ommatidia represent consecutive individuals in one of the bands of larger ommatidia previously mentioned. The band as a whole is cut obliquely, and in such a way that the ommatidia from 1 to 6 are cut successively in deeper or more proximal planes. In ommatidium 1 the rhabdome is surrounded by seven retinular cells, four of which are upon the right side and three upon the left. In addition to these, a large nucleus (*nl. px.*) lies close to the rhabdome. Ommatidium 2 has essentially the same structure as ommatidium 1. In ommatidium 3 the nucleus corresponding to the one seen in ommatidium 1 and 2 is no longer visible, but in its stead there is a small mass of granular protoplasm. A similar mass is also seen in ommatidia 5 and 6. It is usually present directly proximal to the nucleus figured in ommatidia 1 and 2, and is, I believe, the protoplasmic body of the cell to which this nucleus belongs. In ommatidium 4, the seven nuclei of the seven large (functional) retinular cells can be seen. These nuclei appear very large in transverse section compared with the cells in which they occur. It is probable that the cell wall is distended by them, although, owing to the indistinctness of the cell boundaries, I have not obtained positive evidence of this. In ommatidium 6 the seven retinular cells are seen in section at a plane proximal to that in which their nuclei lie. As in ommatidium 1, three of them are upon one side of the rhabdome and four upon the other. In a part of the ommatidium more proximal than that shown in number 6 (Fig. 100), the transverse section of the retinula has the appearance seen in Figure 101. Here the retinular cells have the same relation to the rhabdome that they do in ommatidium 6 (Fig. 100), except in the case of the upper right-hand cell of that figure. This cell enlarges in its more proximal portion, and comes to occupy a position directly below the cell whose nucleus is shown in ommatidium 1 (Fig. 100). The gradual disappearance of this distal cell as one proceeds in a proximal direction from the plane of number 6, Figure 100, to that of Figure 101, and the gradual shifting in the position of the cell which replaces it proximally, can be followed so easily that there is not the least question as to the accuracy of the relations described. It is evident, then, that in Gonodactylus, as in Mysis, the retinula consists of eight cells, one of which is rudimentary.

The *rhabdome* (Figs. 94 and 95, *rhb.*) in Gonodactylus is an elongated rod-like structure of uniform thickness, which extends from the region of the proximal retinular nuclei to the basement membrane. It shows a distinctly toothed edge (Fig. 94), especially in specimens which have been treated with potassic hydrate. In transverse section it is squarish. Owing to its small size, the exact relation of the seven surrounding cells to its four faces cannot be easily determined. The single unpaired cell (Fig. 101) certainly lies opposite a face, not an angle. In this respect it agrees with the unpaired cell in Squilla as figured by Grenacher ('79, Taf. XI. Fig. 122). Probably in Gonodactylus the remaining six cells are related to the sides of the rhabdome as the corresponding ones are in Squilla (compare Grenacher's Fig. 122). In Gonodactylus the retinular cells and rhabdome are in close contact with one another. The separation of these elements as figured by Grenacher in Squilla is probably artificial, as Grenacher himself suggests. In Squilla, according to both Steinlin ('68, p. 17) and Grenacher ('79, p. 125), the rhabdome in transverse sections is subdivided into four equal parts, somewhat as in Mysis. I have not observed this condition in Gonodactylus.

The *distal retinular cells* in Gonodactylus occupy the usual position near the cones. They contain very little pigment, and their number can be determined only by that of their nuclei. These agree with the nuclei of the proximal cells in the possession of a single well defined nucleolus, which is most readily seen in depigmented sections (compare *nl. dst.* and *nl. px.* in Fig. 94). The distal nuclei, especially in the region of the larger ommatidia, are arranged in rows which alternate with the rows of cones (Fig. 99, *nl. dst.*). Although the nuclei are not very definitely arranged, they often show a tendency to be grouped in pairs, and these pairs are so placed that in each row there is evidently one for each adjacent ommatidium. Moreover, in equal lengths of adjoining rows of nuclei and cones, the nuclei are always double the number of cones. I am convinced by these facts that there are two distal retinular cells for each ommatidium.

Besides the cells already described, certain others occur in the proximal part of the retina in Gonodactylus. These are represented by a few small, elongated nuclei (Fig. 94, *nl. ms'drm.*), which are very similar in appearance to certain nuclei occurring in the spaces below the basement membrane. I therefore believe that in Gonodactylus, as in Mysis, the proximal portion of the retina is occupied by intrusive cells, which are probably mesodermic in origin.

The kinds of cells found in the ommatidium of Stomatopods are as

follows: cells of the corneal hypodermis, two; cone cells, four; proximal retinular cells, eight, one of which is rudimentary; distal retinular cells, two; accessory cells (mesodermic?) present.

Decapoda.

I have studied the eyes of the following species of Decapods: Gelasimus pugilator, Latr.; Cardisoma Guanhumi, Latr.; Cancer irroratus, Say; Hippa talpoida, Say; Palinurus Argus, Latr.; Pagurus longicarpus, Say; Homarus americanus, Edw.; Cambarus Bartonii, Fabr; Crangon vulgaris, Fabr.; and Palæmonetes vulgaris, Say. I collected much of this material at the Station of the United States Fish Commission at Wood's Holl, Mass. The specimens of Cambarus were obtained in the vicinity of Philadelphia. I am under obligations to Mr. Herbert M. Richards for specimens of Palæmonetes collected by him at Newport, R. I. A number of eyes of two Crustaceans, Cardisoma and Palinurus, were kindly obtained for me by Mr. Isaac Holden; they were collected on the coast of Florida by Mr. Ralph Munroe, to whom I am indebted for the careful way in which they were preserved.

The *corneal hypodermis* in Decapods was first recognized by Patten ('86, pp. 626 and 642), who observed it in Penæus, Palæmon, Pagurus, and Galathea. Since Patten's announcement of the presence of this layer in Decapods, it has been identified in a number of other genera: in Crangon by Kingsley ('86, p. 863), in Alpheus by Herrick ('86, p. 43), in Astacus by Carrière ('89, p. 225), in Cambarus and Callinectes by Watase ('90, pp. 297 and 299), and in Homarus by myself ('90[a], p. 6). More recently I have observed it also in Palæmonetes (Plate IX. Fig. 103, *cl. crn.*), Crangon, Cambarus, Palinurus, Pagurus, Hippa, Cancer, and Cardisoma.

In almost all Decapods in which the arrangement of the cells in the corneal hypodermis has been observed, these elements have been found to be grouped in pairs, and so distributed that each pair occupies the distal end of an ommatidium (compare Figs. 103 and 106, Plate IX.). This arrangement has been observed, either by others or by myself, in the genera mentioned in the preceding paragraph, except Callinectes, in which the exact arrangement of the cells has not been recorded. Reichenbach's statement ('86, p. 91), that in Astacus there are four hypodermal cells under each facet, is probably erroneous, as Carrière's observations show.

Although Patten was the first investigator who clearly demonstrated the presence of the corneal hypodermis in Decapods, Grenacher, in 1879,

described, I believe, the nuclei of this layer, without however correctly interpreting them. In his account of the ommatidium in Palæmon, Grenacher ('79, p. 123) mentions two kinds of bodies in what he takes to be the distal ends of the cone cells. Of these, the more distal ones (Taf. XI. Fig. 117, *n.*) represent, in his opinion, the nuclei of the cone cells; the more proximal (Fig. 117, *K*^{1}.) he considers as differentiated parts of the cone itself. The positions occupied by these bodies in Palæmon, and by certain bodies which I have observed in Palæmonetes (Plate IX. Fig. 103), are so similar that I believe the structures in the two genera to be homologous. In Palæmonetes the distal bodies lie in the cells of the corneal hypodermis (Fig. 103 *cl. crn.*), and are the nuclei of these cells. They represent what Grenacher considered the nuclei of the cone cells in Palæmon. The proximal bodies in Palæmonetes (Fig. 103, *nl. con.*) are unquestionably the nuclei of the cone cells, yet they correspond to what Grenacher considered the four pieces of the distal segment of the cone. I therefore believe that what Grenacher has described as the nuclei of the cone cells are really the nuclei of the corneal hypodermis, and that what he considered distal segments of the cone are the nuclei of the cone cells.

The *corneal cuticula* in Decapods, in correspondence with the differentiated condition of the corneal hypodermis, is facetted. The outline of the facets is either hexagonal or square. The particular genera in which these different kinds of facets occur have already been mentioned in dealing with the arrangement of the ommatidia in Decapods. The faces of the facets in Decapods are usually very nearly plane, but in Palæmon according to Grenacher ('79, p. 123), and in Palæmonetes (Plate IX. Fig. 103, *crn.*) according to my own observations, the facets are slightly biconvex. In Homarus, as Newton ('73, p. 327) has observed, and in Astacus according to Carrière ('85, p. 167), the distal surface of the facet is plane, the proximal slightly convex. In even the most extreme cases, however, the convexity of the facets in Decapods is not sufficient to make them very effective as lenses.

The facets in Decapods are generally bisected by a fine straight line. This line, as Patten has suggested, probably represents the plane of separation between the two subjacent hypodermal cells. In the square facets this line either divides the facet diagonally, as in Homarus (Parker, '90^a, Fig. 2), or transversely, as in Palæmonetes (Plate IX. Fig. 105). In the hexagonal facets it either bisects opposite sides, as in Cancer (Plate X. Fig. 126), or unites opposite angles, as occasionally in Galathea (Patten, '86, p. 644, Plate 31, Fig. 114). Leydig's ('57, p. 252,

Fig. 134) figure of Astacus, in which each facet is subdivided by *two* diagonal lines into four areas, and Newton's ('73, p. 327) statement that the same condition occurs in Homarus, are probably incorrect.

The *cones* in Decapods are composed of four segments. This number was first observed by Will ('40, p. 13) in Palæmon, and has since been recorded in many other genera. So far as I am aware, there are no Decapods in which the number of segments is not four. As Claparède ('60, p. 194) first pointed out in Galathea and Pagurus, each segment contains a nucleus and represents a single cell. Although the significance of these nuclei was without doubt first fully appreciated by Claparède, it is probable that they were previously seen by Leydig ('55, Taf. XVII. Fig. 31) in the crayfish.

As a rule, the distal termination of the cone cells is on the proximal side of the corneal hypodermis. In the lobster, however, and in Palæmonetes (Plate IX. Fig. 104), the pointed ends of these cells pass between the two cells of the corneal hypodermis, and probably come in contact with the corneal cuticula near the middle of a facet.

It is difficult to determine with accuracy the proximal termination of the cone cells. They can be easily traced to a region immediately distal to the distal end of the rhabdome. In this region, as Schultze ('68, Taf. I. Figs. 9 and 11) has clearly demonstrated in Astacus, the fibrous ends of the four cone cells separate, and pass partially around the rhabdome. In Homarus, these fibres extend proximally, and finally terminate at the basement membrane. A similar method of termination also occurs in Palinurus. In the other genera which I have studied, the fibres, although visible near the distal end of the rhabdome, are lost in the adjacent tissue, and I do not know whether they terminate in this tissue without special attachment, or whether they make their way as excessively fine fibres to the basement membrane. The separation of the fibrous ends of the cone cells, near the distal end of the rhabdome, has been observed by Steinlin ('66, p. 93) in Palæmon, and by Schultze ('67 and '68) in several other Decapods. The statement made by many of the older investigators, and recently reaffirmed by Patten, that the cone and rhabdome are parts of one continuous structure, is without doubt incorrect.

The resolution of the *retinula* into its cellular constituents was first attempted in Decapods by Leydig ('55, p. 408), according to whom the retinula of Herbstia contains four cellular bodies, the nuclei of which can be distinguished in the distal part of the structure. A somewhat similar condition was described by Newton ('73, p. 333) for Homarus;

in this genus, as in Herbstia, it was maintained that there were only four cells. Subsequent investigators have not confirmed this conclusion. In transverse sections of the retinula of Palæmon, Grenacher ('77, p. 32) has demonstrated that the rhabdome is surrounded by *seven* retinular cells. He also ('77, p. 33, and '79, p. 125) observed the same number in the retinulæ of Astacus and Portunus. Since the publication of Grenacher's observations, a retinula containing seven cells has been seen in Astacus by Carrière ('85, p. 169), in Penæus, Palæmon, Galathea, and Pagurus by Patten ('86, pp. 630 and 643), and in Cambarus by Watase ('90, p. 299).

In Homarus, as I ('90[a], p. 21) have already shown, the retinula contains, in addition to the seven functional retinular cells, an eighth rudimentary one, which is little more than a nucleus. In order to ascertain the presence or absence of this eighth cell in other Decapods, I have been careful to record the number of retinular nuclei, as well as the number of functional retinular cells. In some genera, such as Cardisoma and Hippa, I have not been able, on account of the unfavorable condition of the tissue, to make this determination; but in Palæmonetes, Palinurus, Cambarus, Crangon, and Cancer, I have succeeded in ascertaining the number both of the functional cells and of the nuclei in the retinulæ.

In Palæmonetes each rhabdome is surrounded by at least seven retinular cells (Plate IX. Fig. 114, *cl. px.*). The nuclei of these cells usually lie slightly distal to the rhabdome (Fig. 104, *nl. px.*). Their arrangement is shown in Figures 110, 111, and 112, which represent a series of consecutive sections through the region occupied by the proximal retinular nuclei of five ommatidia. The nuclei of the different ommatidia are arranged upon the same plan, and the corresponding nuclei in the different sets have been marked by the same number. In several instances, nuclei have been cut in two, and their parts are found in consecutive sections; in such cases the separate portions have been marked with the same number. As can be seen in these figures, the number of nuclei in the distal portion of each retinula is seven. But in addition to these, there is also another one, which occupies a position near the rhabdome. This nucleus resembles the others in all respects except that it is somewhat longer and narrower. It is drawn in Figure 103 at the level marked 114, and in Figure 114 one can see the regularity with which it occurs. This nucleus is the eighth in the retinula of Palæmonetes, and since it differs somewhat in structure from the other seven, and occupies a more proximal position, I believe it represents a rudimentary retinular cell.

In the distal portion of the retinula in Cambarus there are eight nuclei. The arrangement of these, as seen in successive transverse sections, is shown in Plate X. Figs. 118 to 122. In Figure 118, which represents the most distal section of the series, there are four nuclei, and these are so arranged that there is evidently one for each ommatidium.[1] In the next section (Fig. 119) there are seven nuclei, none of which were seen in Figure 118; the place for an eighth is indicated by an open area, and the eighth nucleus itself is seen somewhat out of place in Figure 120 (*x*). Four of the eight nuclei belonging in Figure 119 are arranged in a manner similar to those in the preceding section, but are not to be confounded with them. The remaining four are so placed that there are two for each ommatidium. Hence in this plane there are, as a whole, three times as many nuclei as there are ommatidia. In the next section (Fig. 120), omitting the nucleus marked *x*, which has been recorded as belonging to the preceding section, there are four nuclei, so arranged that there is one for each ommatidium. In the following section (Fig. 121) the nuclei, omitting the one marked *x*, which will be considered as belonging to the next following section, are so arranged that there are two for each ommatidium. In the last section (Fig. 122), the nuclei are not so regularly grouped as in the previous section, but when taken with the nucleus marked *x* in Figure 121, they constitute a group of four, the arrangement in which is such that each nucleus is intermediate between *four* groups of cone cells rather than between *two*, and therefore in the plane of this section there is one nucleus for each ommatidium. From this enumeration it is evident that the total number of retinular nuclei is eight; namely, one in the first section, three in the second, one in the third, two in the fourth, and one in the fifth. The structure

[1] The nuclei shown in Figures 118 to 122 are arranged upon either the plan shown in Figure 118 or that in Figure 121 (omitting nucleus *x*). Imagine the arrangement in Figure 118 extended over a large surface. The groups of four cone cells could then be regarded as forming lines in the direction of the length of the plate. These lines would alternate with lines of nuclei, and as the nuclei in any line would alternate with the groups of cone cells in an adjoining line, the number of nuclei must equal exactly the number of groups of cone cells; i. e. in this arrangement there is one nucleus for each ommatidium. In a similar way, alternating vertical lines may be constructed from the arrangement in Figure 121. One line would be composed entirely of nuclei situated one opposite each group of cone cells; the other, of alternating nuclei and groups of cone cells. In the former, as well as in the latter, there would be as many nuclei as groups of cone cells. Hence, in this arrangement the nuclei are twice as numerous as the groups of cone cells; i. e. there are two nuclei for each ommatidium.

of these nuclei affords no clue as to which one belongs to the rudimentary cell.

In Palinurus (Plate X. Fig. 125, *nl. px.*), the eighth nucleus is regularly present and easily seen. In Cancer (Fig. 129, *nl. px. 8*) it occupies a position between the adjacent retinulæ. It can also be identified in Crangon.

The retinulæ in Decapods, according to all recent observers, contain seven functional cells. In Homarus, Palinurus, Cambarus, Crangon, Palæmonetes, and Cancer, the retinulæ contain, in addition to the seven nuclei of the functional cells, an eighth nucleus, which represents, I believe, a rudimentary cell. It is probable, therefore, that in all Decapods each retinula really contains eight cells, one of which is rudimentary.

The *rhabdome* in Decapods presents a very uniform structure. It is usually an elongated body, pointed both at its distal and its proximal end, and completely covered, except at its distal tip, by the proximal retinular cells. In those Decapods in which it is large enough to be conveniently observed, its transverse section is squarish, and usually subdivided by two straight lines into four smaller squares (Plate IX. Fig. 113). As Grenacher ('77, pp. 31, 32) first demonstrated in Palæmon, the retinular cells are rather peculiarly arranged around the rhabdome. One of its four sides is flanked by *one* cell, the other three by two cells each. This arrangement can be seen in Palæmonetes (Fig. 113), and probably obtains for all Decapods.

In Palinurus Argus (Plate X. Fig. 124) there appears to be no rhabdome, unless the translucent axial portion of each retinular cell can be said to represent segments of it. The fibrous ends of the cone cells (*cl. con.*) can be easily identified between the retinular cells, but the centre of the retinula is filled with pigment, and shows not the least trace of a rhabdome. This peculiarity of Palinurus was noticed as early as 1840 by Will ('40, p. 15), who described the ommatidium in this genus as being without a transparent mass (= rhabdome).

Although the *distal retinular* cells in Decapods were collectively recognized by Müller ('26, pp. 355, 356) some sixty years ago as a definite pigment band in the distal portion of the retina in the crayfish, they were not identified as separate cells until quite recently. The first investigator to observe them was Carrière ('85, p. 169), who described them in Astacus as a pair of pigment cells flanking each cone. In Cambarus, Crangon, and Homarus, they also cover the sides of the cone, and in the last named genus they are produced proximally into long fibres,

which perhaps pass through the basement membrane. In Palæmonetes (Plate IX. Fig. 108, *cl. dst.*) and in Cancer (Plate X. Fig. 127, *cl. dst.*) they are reduced to pigmented threads, which, starting from comparatively large bases, twine around the lateral surfaces of the cones.

The arrangement and number of the distal retinular cells can be most readily determined from their nuclei. In Cancer (Plate X. Fig. 128) the cells are arranged in circles of six around each group of cone cells; each cell, however, participates in three circles, and consequently there are in reality only twice as many cells as ommatidia. This arrangement of the cells also occurs in Cardisoma, Hippa, and Pagurus. In Crangon (Fig. 123), as I have previously remarked, the nuclei of the distal retinular cells are arranged in rows alternating with the rows of cones. There are twice as many nuclei as cones; hence I conclude that here also there are two distal cells for each ommatidium. In Homarus, Palinurus, Cambarus, and Palæmonetes (Plate IX. Figs. 103 and 109, *nl. dst.*) the nuclei are grouped distinctly in pairs, one pair for each ommatidium.

Each cone in Penæus, according to Patten ('86, p. 634), is surrounded by two pairs of pigment cells, and Watase ('90, p. 299) states that in Cambarus the dioptric part of the ommatidium is sheathed by *four* pigment cells. In Cambarus Bartonii I have been able to find only two such elements, the pair of distal retinular cells already described, and in the other Crustaceans which I have studied I have observed nothing which supports Patten's statement concerning the four pigment cells in Penæus. I am therefore inclined to doubt the accuracy of these two observations.

The interommatidial space in the basal part of the retina in Palæmonetes contains a light pigment similar to that described in the retina of Mysis. Like this the pigment in Palæmonetes is white by reflected light, and yellowish by transmitted light (compare Plate IX. Fig. 115). It is apparently contained within cells (Fig. 103, *cl. ms'drm.*) whose outlines are very irregular, and whose nuclei (Fig. 104, *nl. ms'drm.*) are small and somewhat variable in form. These cells occur on both sides of the basement membrane. As in Mysis, they have probably migrated into the retina, and are perhaps mesodermic in origin. They have been seen by Carrière ('85, p. 169) in Astacus, by Patten ('86, p. 636) in Penæus, and by myself ('90[a], p. 25) in Homarus. I have also recently observed them in Crangon, Cambarus, Cardisoma, Pagurus, and Palinurus, as well as in Palæmonetes.

From what has preceded it is evident that the ommatidium in Decapods contains the following elements: cells of the corneal hypodermis,

two; cone cells, four; proximal retinular cells, eight, one of which is rudimentary; distal retinular cells, two; accessory cells, mesodermic (?) in origin, often present.

Table of Ommatidial Formulæ.

I have now concluded my account of the structure of the ommatidia in Crustaceans, and for the purpose of presenting in a condensed form its more important features I have devised the following table. This consists of a series of ommatidial formulæ constructed upon the plan which I have described in the Introduction. The figures indicate the numbers of particular kinds of cells present in the ommatidium of a given group. The abbreviation *pr.* (present) marks the presence of any kind of cell when the number of that kind is not constant for different ommatidia in the same individual.

Table showing the Cellular Composition of the Ommatidian Crustaceans.

Groups of Crustaceans.	Cells of Corneal Hypodermis.	Cone Cells.	Retinular Cells.			Accessory Cells.
			Undifferentiated.	Differentiated.		
				Proximal.	Distal.	
Amphipoda,	pr.	2	5			pr. (ect.?)
Branchiopodidæ and Apusidæ,	2	4	5			0
Estheridæ,	pr.	5 (4)	5			0
Cladocera,	?	5	5			pr. (ect.?)
Copepoda: Pontella,	pr.	2	5			pr. (ect.?)
Sapphirina,	?	?	3			?
Argulus,	pr.	4	5			?
Isopoda: Idotea,	2	2	6			pr. (ect.?)
Porcellio,	2	2	7			pr. (ect.?)
Serolis,	2 (+?)	2		4	2	pr. (ect.?)
Nebaliæ,	2	4	7			pr. (ect.?)
Schizopoda,	2	2		7 + 1	2	pr. (mes.?)
Stomatopoda,	2	4		7 + 1	2	pr. (mes.?)
Decapoda,	2	4		7 + 1	2	pr. (mes.?)

A few features in the table require explanation. Among the number of cells recorded for the Estheridæ, the figure within the parenthesis

under the head of Cone Cells indicates the occasional occurrence of cones containing only four cells, although the usual number is five. In the line for Serolis, under the head of Corneal Hypodermis, the parenthesis and included signs are intended to indicate the possibility of there being more than two cells in the corneal hypodermis for each ommatidium. In the Schizopods, Stomatopods, and Decapods, the number of proximal retinular cells is expressed in the form of 7 + 1 instead of 8, because one of the cells is rudimentary.

The Innervation of the Retina.

The innervation of the retina in the compound eyes of Crustaceans is chiefly interesting, because of its importance in relation to physiological questions. As this paper deals with a morphological topic, it would be obviously irrelevant to enter upon any extended discussion of this subject. Nevertheless, the innervation of the retina is not without some bearing on the general question which I have set for myself, and I shall therefore not pass it by, but put in as brief a form as possible what I have observed concerning it.

In my account of the retina in the lobster, I described the optic-nerve fibres as terminating in the proximal retinular cells. Near the ganglion each fibre consists of a bundle of fibrils, simply enclosed within a sheath, but as it approaches the retina it becomes coated with pigment. The pigment increases in quantity and the fibre correspondingly enlarges till it finally becomes continuous with the deeply pigmented retinular cell. The fibrillar axis can be distinguished in the pigmented portion of the fibre as a transparent axial structure, and it can also be traced distally through the pigment of each retinular cell till it breaks up into its ultimate fibrillæ, which are spread over the distal half of the rhabdome. This is the method of nerve termination in the lobster, and points very conclusively to the rhabdome as the terminal organ.

What I have seen of the termination of the nerve fibres in other Crustaceans confirms the account which I have already given for the lobster. In some species which I have studied, owing to the small size of the retinal elements, I was unable to determine the cells with which the nerve fibres connected. The termination of the fibres in the cells of the retinula was observed, however, in the following genera: Branchipus, Limnadia, Pontella, Gammarus, Talorchestia, Idotea, Porcellio, Sphæroma, Serolis, Gonodactylus, Mysis, Palæmonetes, Crangon, Cam-

barus, Palinurus, Pagurus, Cancer, and Cardisoma. In the majority of these, a fibrillar axis could be distinguished.[1] In Cambarus, as in Homarus, the nerve fibrillæ spread over the distal portion of the rhabdome.

In Serolis an exceptionally interesting condition is presented. At the level of the basement membrane each retinular cell contains a large fibrillar axis (Plate VI. Fig. 64, *ax. n.*). This becomes somewhat subdivided in the more distal portion of the cell, and in the region of the retinular nucleus it is represented by a cluster of several smaller axes (Fig. 63). At the level of the hyaline cell, these however cannot be distinguished (Fig. 62), but the scattered condition of the pigment granules in this plane is probably to be accounted for by the presence of many separate fibrils in the substance of the cell. In the region of the rhabdome an immense number of fine lines can be seen extending from the retinular cell into the substance of each rhabdomere (Fig. 61). These, I believe, represent the fibrils of the nervous axis. They have been previously observed in Serolis by Watase ('90, p. 291), and are so readily visible that there can be no question as to their presence. Each fibril is perpendicular to the longitudinal axis of the ommatidium, and extends through the rhabdomere to its axial surface. Before reaching this, however, the fibril passes through what seems to be a delicate membrane. When closely examined, this membrane often has the appearance of a row of dots instead of a line, and in several cases I have been unable to discover any traces of it. What its significance is, I am at a loss to say. As I have previously observed, when the elements of the retinula are separated the rhabdomere shows no tendency to break along this line. Since the structure is pierced by the fibrils, and does not appear to be a natural plane of rupture, and since sometimes it is apparently absent, I believe it may be considered, from a morphological standpoint at least, as a secondary and rather unimportant modification within the rhabdomere itself.

If I am correct in maintaining that the nerve fibrils in Serolis terminate in the rhabdomere, it is probable that they have a similar method of ending in all other Crustaceans, and in such instances as Homarus, where they have been traced only to the surface of the rhabdome, their actual termination has probably not been seen.

[1] A definite fibrillar axis was traced from below the basement membrane to the region of the rhabdome in Gammarus (Plate I. Figs. 6–8), Porcellio (Plate V. Fig. 46), Idotea (Plate V. Figs. 53 and 55–57), Mysis (Plate VII. Figs. 87–89), Gonodactylus (Plate VIII. Figs. 101, 102), Palæmonetes (Plate IX. Figs. 116, 117), Cambarus, Pagurus, Cancer (Plate X. Figs. 130 and 131), and Cardisoma.

The termination of the fibrillæ of the optic nerve in the rhabdome supports Müller's belief that the nerve fibres terminate in a region near the proximal ends of the cones, and Grenacher's more specific view that they are connected with the retinular cells, and that the rhabdome is the terminal organ. This method of termination is not consistent with the opinion of Gottsche and Leydig, that the cone is the terminal organ, nor with Patten's rather similar belief that the ultimate nerve fibrillæ are distributed to the cone. I am therefore compelled to think that these authors are mistaken in their conclusion.

Theoretic Conclusions.

In attempting to account for the variation in the number of cells in different types of ommatidia, two courses naturally suggest themselves. Either the different kinds of ommatidia vary in the number of cells which they contain, because they have had separate origins, or they are different because in some or all of them the ancestral ommatidium has suffered modification. An examination of the table on page 115 shows conclusively, I think, that in Crustaceans even the most extreme types are so little removed from one another that it is much more probable that the different kinds of ommatidia are genetically connected, than that they have been produced independently. Granting this statement, the question naturally arises, What are the means by which the primitive ommatidium was modified? I believe that a close scrutiny of the cellular structure of the ommatidia in living Crustaceans will disclose some of the factors in this process. There are at least three of these to be distinguished: the differentiation of cells, the suppression of cells, and the increase in the number of cells by cell division.

By the differentiation of cells, I do not mean the process by which hypodermal cells have become converted into retinular or cone cells, but that by which an element already differentiated in the ommatidium is secondarily modified to subserve another function. The only instance of this kind with which I am acquainted occurs among the retinular cells. In the majority of the simpler Crustaceans, the sides of the cones are covered with pigment, which is almost always contained in the distal ends of the retinular cells. In Serolis, among the Isopods, and apparently in all the genera of Stomatopods, Schizopods, and Decapods, the cones are surrounded by special pigment cells. These are always twice as numerous as the ommatidia, and represent, I believe, retinular cells which have become differentiated for the special purpose of sheathing

the cones. The way in which this differentiation may have occurred has already been suggested in my paper on the lobster ('90', p. 57).

Although I have expressed the opinion that these cells are to be regarded as modified retinular cells, it might be maintained that they are merely enlarged accessory pigment cells, such as occur in the interommatidial space of many Crustaceans. But I believe such an interpretation of these cells would be erroneous, for the following reason. In Serolis the nuclei of the pigment cells which surround the cone (Plate VI. Fig. 65, *nl. dst.*) possess one, and sometimes two, well marked nucleoli, but no fine chromatine granules. In this respect they closely resemble the nuclei of the proximal retinular cells (*nl. px.*), and differ considerably from those of the accessory pigment cells (*nl. h'drm.*). The nuclei of the last named cells contain only fine granules. So far, then, as their nuclei are concerned, the distal retinular cells bear a much closer resemblance to the proximal cells than to the accessory pigment cells. Each retinula in Serolis contains, moreover, only four cells, and in this respect differs considerably from other Isopods, where the number of retinular cells is either six or seven. On the supposition that the pigment cells surrounding the cone in Serolis are accessory pigment cells, one would be called upon to account for the exceptionally small number of cells in the retinula of this genus; whereas, if the cells around the cone are regarded as modified retinular cells, they may be taken to indicate for Serolis a primitive retinula composed of six cells, a number characteristic of the retinulæ in other Isopods. This interpretation of the condition of the retinula in Serolis is borne out by what is known of the retinula in Sphæroma, where, it will be remembered, a transition between the condition in Serolis and that in other Isopods was distinctly indicated.

In the Stomatopods, Schizopods, and Decapods, if my observations are correct, there are no ectodermic accessory pigment cells. Consequently, a comparison between these cells and what I have called the distal retinular cells cannot be drawn. In Mysis (Plate VII. Fig. 73), Gonodactylus (Plate VIII. Fig. 94), and Palæmonetes (Plate IX. Fig. 103), as well as in all other Decapods which I have examined, the resemblance between the nuclei of the retinular cells and those of the pigment cells which surround the cone is as striking as in Serolis, and suggests the origin of these cells from retinular cells rather than from any other source. In Homarus, the pigment cells around the cone present a condition of some interest in this connection. Each pigment cell is extended proximally as a long fibre, which certainly reaches nearly to the base-

ment membrane, and probably passes through it in company with the fibrous ends of the retinular cells (compare Parker, '90[a], pp. 17–19). Admitting that these cells are merely modified accessory pigment cells, such a condition as this is quite unintelligible to me; but granting them to be differentiated retinular cells, their fibrous extensions can be easily explained as the rudiments of the fibrous portion of the cell with which the nerve fibre was once connected. A somewhat similar case occurs in Mysis, where the centre of each of the pigment cells which surround the cone contains a small transparent axis. This axis in every respect except that of connection with a nerve fibre corresponds to the fibrillar axes described in the functional retinular cells of this Crustacean (compare Plate VII. Figs. 77, 78, and 87). Consequently, the axis in the distal cells either represents a rudimentary nervous axis, in which case the cell containing it must be regarded as a retinular cell, or it is something for which I can suggest no explanation.

These facts lead me to conclude that the pigment cells which surround the cone in Serolis, the Stomatopods, Schizopods, and Decapods, are to be regarded as modified retinular cells, and I have therefore described them under the name of distal retinular cells, in contrast to proximal retinular cells, or those which retain their primitive position around the rhabdome. In the differentiation of a group of simple retinular cells into proximal and distal cells, the latter necessarily change their function from that of terminal nervous organs to that of screens chiefly concerned in excluding the light from the sides of the cones. Wherever the distal retinular cells occur, they afford evidence, I believe, that the structure of the ommatidium has undergone a modification from the primitive ommatidial condition.

The second method by which the structure of ommatidia may be changed, namely, the suppression of cells, is perhaps the one whose presence is most easily detected because of the frequent persistence of the partially reduced cells. These rudimentary cells can be identified most readily in the cases where they belong to groups in which the number of elements is constant for different ommatidia. I know of no evidence of suppression among the groups of cells in the corneal hypodermis or the cones. Among the retinulæ, however, it seems to be of rather common occurrence. The first indication of this process is naturally a diminution in the size of the cell to be suppressed. Such a step is perhaps shown in the retinula of Gammarus (Plate I. Fig. 6), where one of the five cells, although evidently functional, is nevertheless considerably reduced. Without much doubt, the body described in the

retinula of Idotea robusta represents, for reasons already stated, the seventh cell present as a functional structure in Porcellio. In Idotea irrorata the retinulæ, with very few exceptions (Plate V. Fig. 54), contain only six cells, showing no trace of the seventh cell. This condition, I believe, is to be interpreted as one in which a cell has been completely suppressed. In Stomatopods, Schizopods, and Decapods the retinulæ have been shown to contain, in addition to the nuclei of the seven functional cells, an eighth nucleus, which may represent a rudimentary cell.

In all of the cases thus far cited, it might be maintained that what I have considered rudimentary cells are really cells newly acquired by the ommatidia, and not old cells gradually undergoing suppression. The condition in Idotea, however, where the body in question apparently contains no nucleus, would be difficult to explain on this assumption, whereas, if it be considered a cell undergoing reduction, its condition can be easily accounted for. In Stomatopods, Schizopods, and Decapods, the constancy in the number of cells and in the position of the eighth nucleus, the small amount of protoplasm which surrounds it, and the striking resemblance which it has to the other retinular nuclei, are facts difficult to explain on the assumption that it represents a newly acquired cell, but easily accounted for on the supposition that it is the remnant of a partially suppressed cell. For these reasons, I believe that the instances cited are valid cases of partial suppression, and that this must be regarded as one of the actual means employed in the modification of ommatidia.

That ommatidia have been modified by an increase in the number of their cells by cell division, is a proposition not easily established. The difficulty of obtaining conclusive evidence on this point can be made clear by an example. Let it be assumed that cones composed of two cells are converted by the division of the cells into cones composed of four cells. This step, even when first taken, would probably be accomplished during the embryonic growth of an animal, and therefore before the cones themselves had begun to be differentiated. What would actually happen would probably be this: the two cells, the homologues of which in all previous animals had given rise to two cone cells, would in this case each divide, thus producing a group of four cells, which ultimately would form a cone of four segments. If we could compare the adult animal in which such a process had occurred for the first time with its immediate ancestors, the only important difference that would be observed would be in the number of the cells in each cone, and if the genetic relations of the two individuals were not known, it could not be stated with certainty whether in

one case we were dealing with an animal which had lost two cone cells or in the other, with one which had gained two; in other words, it would be impossible to determine which of the two conditions was the primitive one. The importance of embryological evidence in determining this question must therefore be apparent. But evidence from even this source might not be conclusive. Thus in the development of the lobster I have traced in detail the steps by which the ommatidia are formed, and although in this Crustacean the considerable number of cells in each ommatidium would warrant one in expecting some evidence of increase by division, the division of the cells in the retina is entirely accomplished some time before these elements show any grouping into ommatidia. Hence, the exact method of origin of the cells of the ommatidium cannot at present be given. I have observed that the same is also true in Gammarus; cell division is completed before the cells are grouped into ommatidia. Perhaps in the development of some other Crustaceans evidence of the kind which I have sought may be obtained, but in the few species which thus far have been studied the evidence has not been produced.

Although the supposition that ommatidia may increase the number of their cells by the division of those which they already possess is not supported by any direct observations with which I am acquainted, there are some facts recorded which are indirectly confirmatory of it. Thus, in Phyllopods, an increase in the number of cone cells appears to accompany a progressive differentiation of the retina itself. In this group, as I have already pointed out, the simplest condition of the retina is found in Branchipus and Apus. From the retina of Apus that of the Estheridæ can be easily derived, and the retina in the Estheridæ represents a condition from which the retina of the Cladocera may have arisen. That this series of retinas, from Apus through the Estheridæ to the Cladocera, is a natural one is abundantly proved by the course taken in the development of the eye in these groups. If we regard the condition of the cones in these Crustaceans, we shall find that in the most primitive retina, that of either Branchipus or Apus, they consist of four cells; that in the more complex retina of the Estheridæ they are usually composed of five cells, although cones of four cells are not unfrequent occurrences; and finally, that in the Cladocera they are always composed of five cells. Apparently in this series the development of the retina is paralleled by a corresponding development in the cones, whereby one composed of four cells is ultimately converted into one with five cells. Since the resemblance between any two of the cells in a cone composed

of five elements is quite as close as that between the cells in cones containing only four elements, I believe that the additional cell, which has increased the number of segments from four to five, has been derived by the division of one of the original four cone cells, and not from an extra-ommatidial source.

Another instance of this kind occurs among the Isopods. The cones in this group, it will be remembered, are usually each composed of two segments. According to Beddard's figures ('90, Plate XXXI. Figs. 1 and 4) in Arcturus, however, they occasionally consist of three segments, and in Asellus aquaticus, according to Sars ('67, p. 110), although three of the four cones in each eye are composed of only two segments each, the fourth regularly contains three. The size of the segments in the fourth cone differs; two are small, and together their bulk about equals that of the third, and the last is approximately of the size of a segment in one of the other cones. If we attempt to explain the condition of the cone composed of three segments by supposing it to have been produced by adding to the normal pair of cone cells a single cell from some source external to the ommatidium, we are met with the difficulty, that what is apparently the added cell — the larger one — resembles more closely a segment in the other cones than do either of the two remaining cells, although the latter must on this assumption represent the original segments. If, however, we imagine the small segments to have arisen by the division of a single larger one similar to the large one which remains in the cone, the relation of the resulting segments both in size and number is a perfectly natural one. This explanation, therefore, seems to me to be more probable than the former. For these reasons, I believe that an increase in the number of cells in an ommatidium takes place by the division of the cells already forming a part of that ommatidium, rather than by the importation of new elements hitherto foreign to the ommatidium.

The conclusion which I would draw from the preceding discussion is, that there are at least three means of modifying the numerical formulæ of ommatidia, all of which involve only the cells primitively belonging to the ommatidium, and therefore do not necessitate the introduction of new cells from extra-ommatidial sources. They are cell differentiation, cell suppression, and cell multiplication.

Having now determined the means by which the cellular structure of the ommatidia in living Crustaceans is modified, we are prepared to approach the question of the structure of the primitive ommatidium. If it could be shown that ommatidia were modified only by increasing the

number of their elements, it would naturally follow that those composed of the fewest cells would more nearly resemble the ancestral type than those which consist of many cells. On the other hand, if the suppression of cells were the only means employed in modifying structure, the ommatidia containing the greatest number of elements would most nearly approach the primitive type. Since, as I believe, both means are employed in the Crustacea, the determination of the structure of the ancestral ommatidium is evidently a difficult problem. Perhaps the most satisfactory way of attempting its solution is to consider separately the different categories of cells which enter into the formation of an ommatidium, and, after reviewing the conditions presented by each in different Crustaceans, to determine, if possible, which of these conditions is the most primitive. The conclusions thus arrived at concerning each kind of cell will afford the necessary grounds for the construction of an hypothetical formula of the ancestral ommatidium. Although it is not necessary that this ommatidium should be represented in any living Crustacean, for the ommatidia in all these may have suffered modification, yet it is possible that a representative of it may still exist.

Turning now to the consideration of the different groups of cells, we find that the corneal hypodermis presents two conditions; one in which its cells are not regularly arranged, and another in which they are grouped in pairs, each pair lying at the distal end of an ommatidium. The latter condition is characteristic of the Decapods, Schizopods, Stomatopods, Nebaliæ, Isopods, and some Branchiopods; the former, so far as is known, occurs in the Amphipods, the Branchiura, and in some Branchiopods (Limnadia and some species of Branchipus). In view of the fact that the corneal hypodermis is a part of the retina which retains the function of the general hypodermis but slightly modified, and that in the latter the cells do not present a regular arrangement, it is probable that a corneal hypodermis in which the cells are not regularly arranged is of a more primitive character than one in which they are definitely grouped.

The number of cells in the individual cones of Crustaceans varies from two to five. Cones composed of two cells occur in Eucopepoda, Amphipods, Isopods, and Schizopods; cones of three cells are present only exceptionally in Isopods; cones of four cells are found in the Decapods, Stomatopods, Nebaliæ, Branchiura, and some Branchiopods; cones of five cells characterize the Cladocera and some Branchiopods. I have already given reasons for regarding the cones composed of three cells as having been derived from those containing two, and cones com-

posed of five cells from those possessing four. Since there is no evidence of degenerate cells in any of the cones composed of two segments, I am convinced that cones with four cells are derived from those with two cells, and not the reverse. On these grounds, I conclude that the most primitive form of cone in living Crustacea is that consisting of two cells.

The retinular cells in Crustaceans are subject to considerable variation. As I have previously shown, an ommatidium may contain one or two kinds. When there is only one kind, all the cells are grouped around the rhabdome, and are known simply as retinular cells. When there are two kinds, one occupies a position around the rhabdome, and the other around the cone ; the former I have called proximal retinular cells, the latter distal retinular cells. Proximal and distal retinular cells occur in Serolis, the Stomatopods, Schizopods, and Decapods ; simple retinular cells apparently characterize the ommatidia of all other Crustaceans. I have already presented reasons for considering the distal retinular cells as modified simple retinular cells, which, in the separation of the cone from the rhabdome by the elongation of the ommatidium, have lost their connection with the nervous element, but have retained their place next the dioptric one. A group of retinular cells in which this differentiation has occurred is not so primitive in its structure, therefore, as one in which all the retinular cells retain their original position around the rhabdome, as in the groups of Crustacea which possess simple retinular cells.

The number of simple retinular cells in Crustacean ommatidia varies from five to seven. In Nebalia, and some Isopods, the retinula contains seven cells ; in other Isopods it is composed of six cells, and in the Branchiopods, the Cladocera, some Copepods, and Amphipods it consists of five cells. It is difficult to state which of these numbers represents the primitive condition. In the Isopods, as I have previously indicated (pp. 86 and 87), there is considerable evidence to show that a retinula composed of six cells has been produced from one containing seven by the suppression of one cell. Possibly in this way the retinula with five cells was derived from that with six, but I know of no observations which favor this supposition.

A small amount of indirect evidence on this question is to be obtained from the other structural peculiarities of the ommatidia containing retinulæ with five, six, or seven cells. These retinulæ occur in connection with two kinds of rhabdomes, — one in which the rhabdomeric segments are easily distinguishable, and the other from which they are apparently absent. Of these two kinds, the one in which the

segments persist is evidently more primitive than the one in which their outlines are obliterated.

Probably in Nebalia, in which the retinula is composed of seven cells, and certainly in Idotea, where it consists of six, the rhabdome shows no indication of being composed of rhabdomeres, but in Porcellio the seven retinular cells surround a rhabdome composed of a corresponding number of rhabdomeric segments. In Branchipus, the retinula consists of five cells, but the rhabdome is apparently not composed of separable rhabdomeres, whereas in Pontella, Argulus, Gammarus, Talorchestia, Hyperia, and Phronima the five retinular cells are each represented by a rhabdomere. The more frequent occurrence of a primitive condition of rhabdome with the retinula having five cells than with that having seven, favors indirectly the idea that the retinula with the smaller number of cells is the more primitive of the two. The types of cones associated with the two kinds of retinulæ offer almost no evidence on the question in hand. Thus, a retinula of seven cells is associated with a cone of four cells in Nebalia, and with one of two cells in Porcellio, and a retinula of five cells is combined with a cone of four cells in Branchipus and Argulus, and with one of two cells in Amphipods. The relation of the two kinds of retinulæ to the corneal hypodermis affords some slight evidence in support of the opinion that the retinula of five cells represents the more primitive type; for although the differentiated type of corneal hypodermis — the one in which the cells are regularly arranged — may occur with either type of retinula, the undifferentiated hypodermis — in which the cells are not regularly grouped — is known to be associated only with retinulæ containing five cells (some Branchiopods, Argulus, and Amphipods). The evidence drawn from these various sources is obviously very slight; but such as it is, it indicates that the retinula with five cells, rather than that with a greater number, represents the more primitive condition. This conclusion receives some additional support from the fact that the retinula composed of five cells characterizes the ommatidia in a number of not otherwise very closely related Crustaceans (Pontella, Argulus, the Branchiopods, and Amphipods), whereas the type possessing seven cells occurs only among certain Isopods and in the Nebaliæ. I believe, therefore, that all the evidence at present deducible from the condition of the simpler retinulæ indicates that the one which contains five cells is more primitive than that composed of six or seven cells.

In the present argument I have purposely omitted any mention of the condition of the retinula in the Corycæidæ, those Copepods in which the

lateral eyes present a highly modified condition. I have done this because I believe that the lateral eyes in many Copepods are degenerate, and that therefore the evidence to be drawn from them cannot be as trustworthy as that from other sources. That the lateral eyes in Copepods are degenerate, is shown from the fact that in many members of the group the eyes are entirely absent, and that in those in which they do occur, their structure is subject to considerable variation. Thus in Pontella the retina contains, besides one group of five retinular cells, three isolated nervous cells, whereas in Sapphirina there is a group of three retinular cells, and at least one isolated nervous cell. In Pontella, Sapphirina, Corycæus, and Copilia each retina is provided with a single lens, but in Irenæus, according to Claus ('63, Taf. II. Fig. 1), there are two lenses in each eye. These variations, including the total disappearance of the organ in some members of the group, lead me to believe that the lateral eyes in the Copepods are degenerated, and therefore are organs in which the suppression of cells may have reduced them to even a simpler condition than that presented by the ancestral ommatidium.

The conclusion which I draw from the preceding argument is, that the type from which the ommatidia in all living Crustaceans are probably derived would exhibit the following structures: a corneal hypodermis in which the cells are not regularly arranged, and consequently an unfacetted corneal cuticula; a cone composed of two cells; a retinula composed of five retinular cells and having a rhabdome which consists of five rhabdomeres. The retina of the primitive eye, a simple thickening in the superficial ectoderm, would be composed of ommatidia of this type arranged upon the hexagonal plan. None of the Crustaceans with which I am acquainted possess an eye of exactly this structure. The one in which this condition is most nearly represented is perhaps Gammarus. In this animal all the requirements of the hypothetical eye are fulfilled, except that the form of the retina as a whole is somewhat disturbed by the separation of the corneal hypodermis from the layer of the cones and retinulæ by a corneo-conal membrane, and by the partially disguised condition of the basement membrane.

If my conclusions be correct concerning the structure of the primitive ommatidium and the means by which it has been modified, it follows that the principal types of ommatidia have been produced mainly by increasing the number of cells in the primitive type, and that, of the three means of modifying the structure of ommatidia, cell division has been the most influential.

Although the hypothetical ommatidium which has been described in

the preceding paragraphs has been spoken of as ancestral, it is not to be supposed that the condition which it presents must be regarded as necessarily its simplest form. I feel tolerably confident, however, that the primitive ommatidium must have been at least as simple as I have assumed it to be. Possibly its retinula may have been composed of less than five cells, as is that seen in some Copepods; although, as I have previously remarked, the condition of the lateral eyes in these Crustaceans is probably influenced by degeneration, and therefore may not represent a primitive stage. What might be regarded, however, as a more primitive form of ommatidium than that which I have described, may be seen in the eye of the Chætopod Nais (Carriere, '85, pp. 28, 29). In this worm the eye lies in the hypodermis on the side of the head, and consists of a few relatively large transparent cells, the proximal faces of which are in part covered by pigment cells. It is probable that the transparent cells are merely dioptric in function, and that the pigment cells are nervous. The transparent cells may therefore be looked upon as the forerunners of cone cells, and the pigment cells at their bases as retinular cells not yet differentiated into a retinula. It is not difficult to imagine the origin of an ommatidium from a single one of the transparent cells and its accompanying pigment cells, and, by an increase in the number of such groups, the production of a retina like that of the compound eye of Arthropods.

This view of the origin of the ommatidia in Arthropods is irreconcilable with that recently advanced by Watase ('90), according to whom each ommatidium is to be regarded as a pit formed by an involution of the hypodermis. The supposed cavity of this pit occupies nearly the whole length of the axial portion of the ommatidium, and is filled by the secretions of the cells constituting its wall. The secretion in the deeper part of the pit forms the rhabdome; that which is produced nearer its mouth, the cone. During the formation of the pit, the hypodermal cells are believed to retain such mutual relations that their morphologically distal ends lie next its cavity; hence the secretions produced by these ends, the rhabdome and cone, are to be regarded as modifications of the chitinous cuticula of the outer surface of the body.

Ingenious as this theory is, I have not been able to convince myself of its tenability. It may be urged against the assumption that the retinular cells occupy a proximal position and the cone cells a distal one on the wall of a hypodermal pocket, that in Gammarus the retinular cells extend from the distal to the proximal face of the retina, and that in Homarus the cone cells have a corresponding extent; these conditions show that

it is possible to interpret the cells in an ommatidium as elements in a thickened epithelium, all of which originally extended from one face of the layer to the other, and the grouping of which is not even now interfered with by any process of involution. But granting that the retinal cells are thus arranged, it must be admitted that the surface on which the rhabdomeres are produced corresponds to the *sides* of the cells rather than to their *distal ends*. This interpretation of the position of the rhabdome is not, so far as I am aware, contrary to any well established facts, and indeed it is rather more in accordance with the condition seen in the eyes of some Arthropods than that implied in Watase's theory. Thus, in the lateral eyes of scorpions the retinal cells are arranged as in an ordinary epithelium, and the lateral wall of each cell is in part occupied by a rhabdomere. In this instance, then, it must be admitted either that the rhabdomeres are produced on the *sides* of the retinal cells, or that each cell has independently rotated upon itself, so as to bring its morphologically distal end into a position corresponding to the side of an ordinary epithelial cell. But there is neither direct evidence to show that this rotation of single cells has occurred, nor, in this case, can there be any motive assumed which might have induced the rotation of single elements. I therefore believe that in the lateral eyes of scorpions the rhabdomes are on the sides of the retinal cells in the strictest morphological sense; and if they can occur in this position in the eyes of scorpions, I can see no reason why they might not occur in similar positions on the retinal cells of compound eyes. Hence it seems to me as reasonable to interpret the retina in compound eyes as a layer of modified epithelium unaffected by involutions, as it is to consider it a layer in which each ommatidium represents an infolding.

When, moreover, an attempt is made to show how a particular ommatidium has arisen by involution, some difficulties are encountered. Thus in Gammarus, in which the ommatidium is of a primitive type, each ommatidial pocket would involve seven cells, two of which, the cone cells, must be imagined as forming the neck of the involution, while the remaining five, the retinular cells, would constitute the deeper portion of the pocket. The mechanical difficulty which would accompany the formation of an involution involving so small a number of cells must be obvious, and offers, I believe, an obstacle to the successful operation of the process assumed in Watase's theory.

The one instance in which Watase has described an actual involution to form the eyes in Arthropods is the lateral eye of Limulus. These eyes consist of a cluster of hypodermal pits, over each of which there is a cu-

ticular lens. Although there cannot be the least doubt that in this case each pit is a hypodermal involution, the belief that each one is homologous with an ommatidium is by no means so well founded. In structure the wall of the pit differs considerably from that of an ommatidium; it contains no cells which can be definitely denominated, either as cone cells or as cells of the corneal hypodermis, and it does contain a large ganglionic cell, which is only questionably homologous with any element in an ommatidium. In most respects in which these pits differ from ommatidia, they resemble simple eyes, and I therefore regard them as such, rather than as representatives of an early condition in the formation of an ommatidium.

When to the objections raised in the preceding paragraphs the statement is added, that in both Homarus and Gammarus — representatives of the extremes of organization — the ommatidia are developed without showing any trace of infolding, Watase's theory of the formation of ommatidia by means of involutions appears in a still less favorable light. I therefore regard ommatidia, not as the result of involutions, but as differentiated clusters of cells in a continuous unfolded epithelium.

I have not observed anything that would lead to the conclusion recently expressed by Patten ('90), that an ommatidium is a hair-bearing sense bud. I believe, on the contrary, that they have had a very different origin.

In conclusion, I may add, that if my idea of the origin of ommatidia be correct, it supports Grenacher's opinion, that compound eyes are not derived directly from aggregations of simple eyes, but from groups of optic organs which were even more primitive in their structure than simple eyes. Possibly such primitive organs were the antecedents of both the compound and simple eyes of Arthropods, as Grenacher suggests; but possibly the two kinds of eyes may have had totally different origins.

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EXPLANATION OF FIGURES.

All the drawings were made with the aid of an Abbé camera. Unless otherwise stated, the specimens from which the drawings were made were stained in Czokor's alum-cochineal and mounted in benzol-balsam. The reagent used in depigmenting sections was an aqueous solution of potassic hydrate $\frac{1}{4}\%$.

ABBREVIATIONS.

a.	Anterior.
ax. n.	Axis of nerve fibrillæ.
brs. oc.	Optic pocket.
cl. con.	Cone cell.
cl. crn.	Cell of corneal hypodermis.
cl. dst.	Distal retinular cell.
cl. hyl.	Hyaline cell.
cl. ms'drm.	Mesodermic cell.
cl. px.	Proximal retinular cell.
cl. rtn.'	Retinular cell.
cl. rud.	Rudimentary retinular cell.
cnch.	Shell.
cœl.	Body cavity.
con.	Cone.
cp. sng.	Blood corpuscle.
crn.	Corneal cuticula.
cta.	Cuticula.
d.	Dorsal.
dsc.	Sucking disk.
dx.	Right.
gn. opt.	Optic ganglion.
h'drm.	Hypodermis.
hp.	Liver.
in.	Intestine.
lns.	Lens.
mb. ba.	Basement membrane.
mb. crn.	Corneal membrane.
mb. crn'con.	Corneo-conal membrane.
mb. i'cl.	Intercellular membrane.
mb. n. opt.	Membrane of optic nerve.
mb. pi'ph.	Peripheral membrane.
mb. pr'con.	Preconal membrane.
mu.	Muscle.
n. fbr.	Nerve fibre.
nl. con.	Nucleus of cone cell.
nl. crn.	Nucleus of cell in corneal hypodermis.
nl. dst.	Nucleus of distal retinular cell.
nl. h'drm.	Nucleus of hypodermal cell.
nl. hyl.	Nucleus of hyaline cell.
nl. ms'drm.	Nucleus of mesodermic cell.
nl. px.	Nucleus of proximal retinular cell.
nl. rtn.'	Nucleus of retinular cell.
n. opt.	Optic nerve.
oc.	Eye.
omm.'	Ommateum.
p.	Posterior.
po. brs.	Pore of optic pocket.
r.	Retina.
rhb.	Rhabdome.
rhb'm.	Rhabdomere.
rtn.'	Retinula.
s.	Left.
v.	Ventral.
va sng.	Blood-vessel.

Such other abbreviations as have been used are explained in the description of the figures with which they occur.

PLATE I.

Gammarus.

Fig. 1. A section of the right eye in a plane transverse to the chief axis of the body and through the central part of the retina. × 115.

" 2. A section lengthwise of an ommatidium. The numbers at the left of the figure correspond to the numbers of the six following figures of transverse sections, and mark the levels at which the latter were taken. × 475.

" 3. A transverse section in the plane of the corneal hypodermis. × 475.

" 4. A transverse section through the distal ends of the retinular cells and cone. × 475.

" 5. A transverse section through the proximal portion of the cone and through the adjoining retinular cells. × 475.

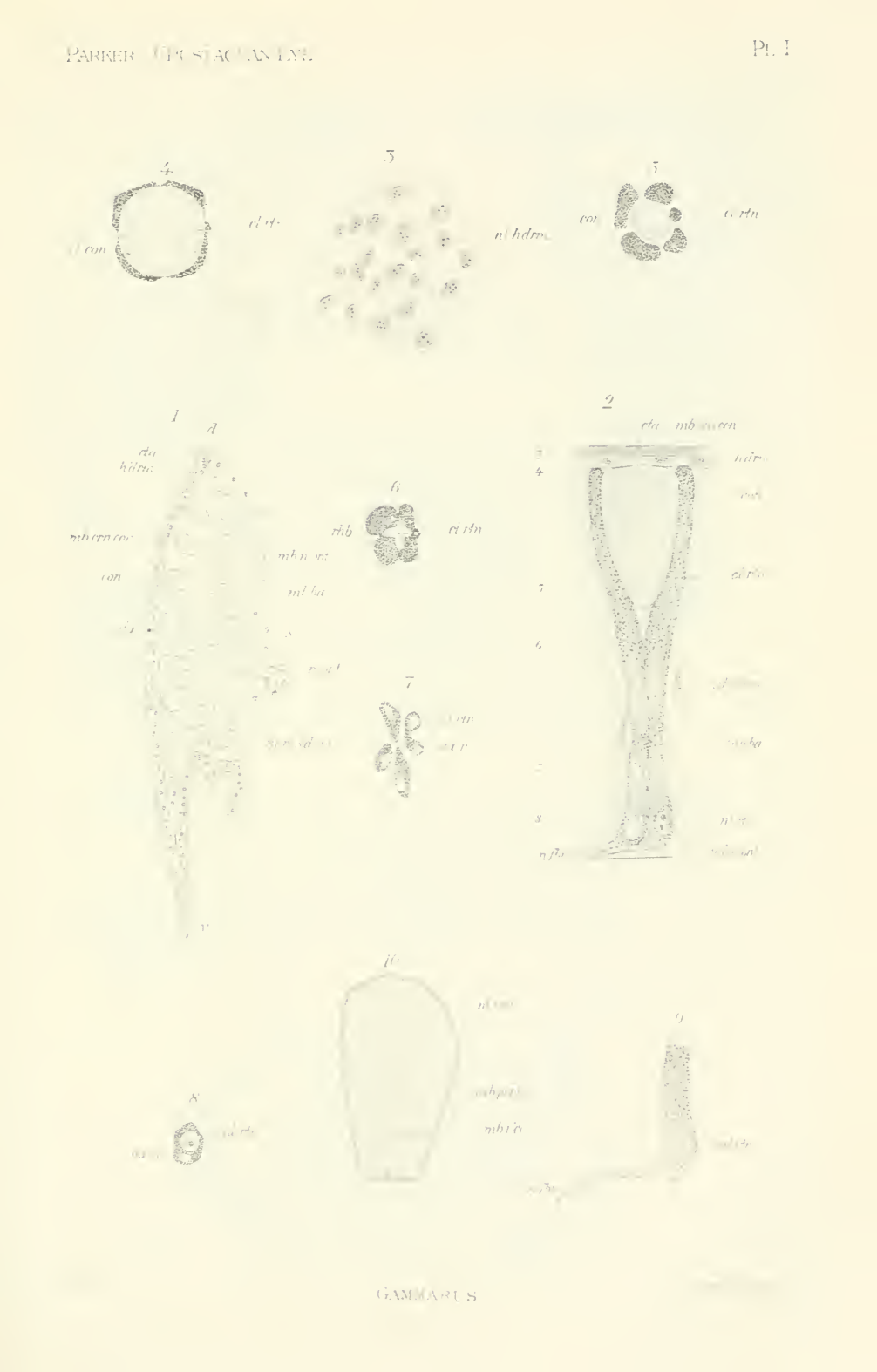
" 6. A transverse section through the retinula in the region of the rhabdome. × 475.

" 7. A transverse section through the retinular cells somewhat proximal to the basement membrane. × 475.

" 8. A transverse section through a single retinular cell in the region of its nucleus. × 475.

" 9. The proximal portion of a retinular cell viewed from the side. (Compare Fig. 2.) Isolated in Müller's fluid. Not stained. × 475.

" 10. A cone isolated in Müller's fluid and viewed from the side. Not stained. × 475.



GAMMARUS

PLATE II.

Argulus.

(Figs. 11–17.)

Fig. 11. A section in a plane transverse to the chief axis of the body and through the right eye. Depigmented. × 140.

" 12. A longitudinal section of an ommatidium. × 475.

" 13. A longitudinal section of an ommatidium which had been depigmented The numbers at the left of the figure correspond to the numbers of the four following figures of transverse sections, and mark the levels at which the latter were made. × 475.

" 14. A transverse section through the distal end of a cone and the surrounding pigment cells. × 475.

" 15. A transverse section through the proximal portion of a group of four cone cells. The intercellular membranes of the cells present four thickened regions. × 475.

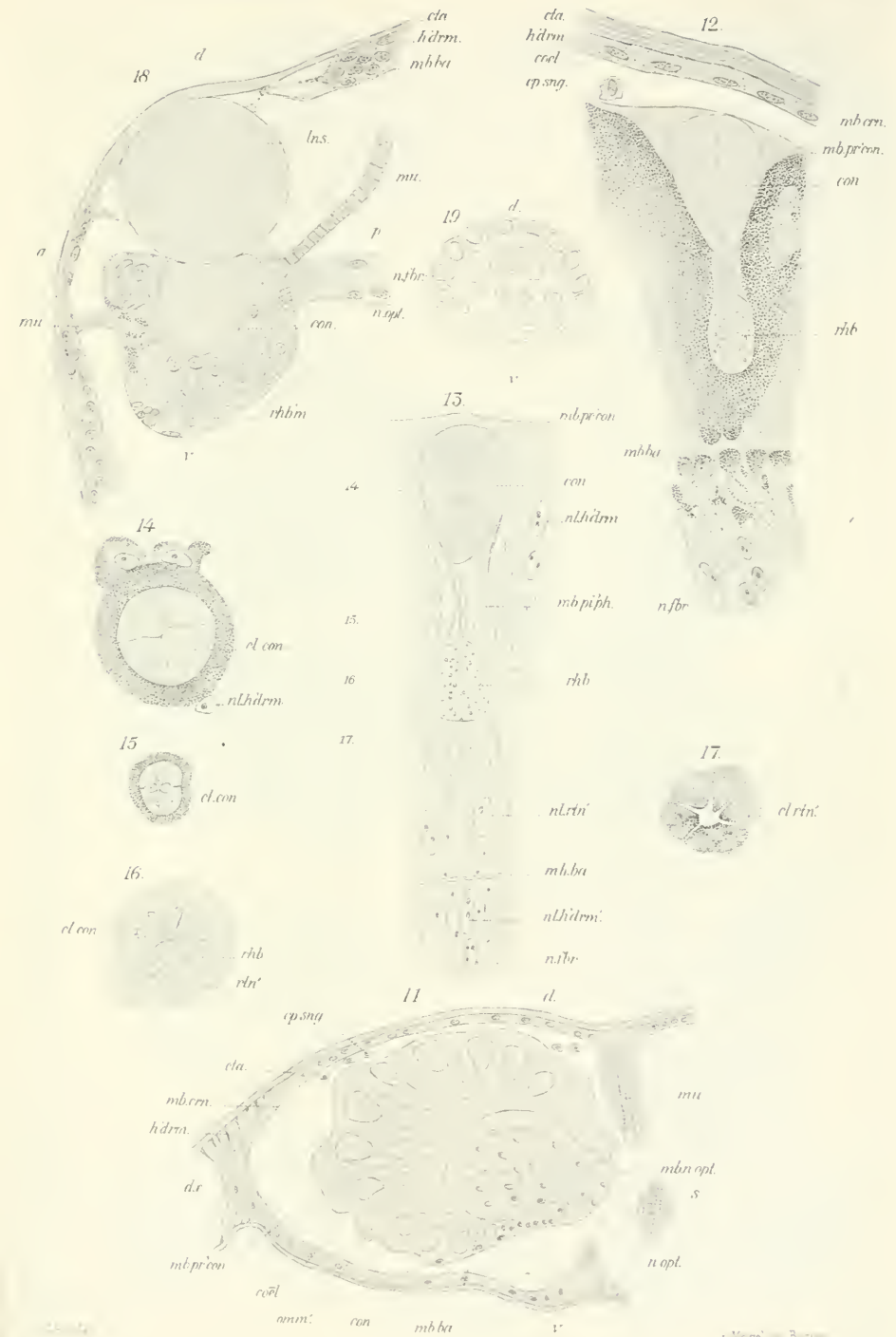
" 16. A transverse section through the rhabdome. Depigmented × 475.

" 17. A transverse section through the retinula somewhat proximal to the rhabdome. × 475.

Pontella.

Fig. 18. The left lateral eye seen from the left side. The section is an optical one; its plane is very nearly parallel to the sagittal plane of the body. Depigmented in alcohol (see p. 78). × 275.

" 19. A transverse section of the optic nerve from a region immediately posterior to the retina. The sagittal plane divides the nerve into symmetrical halves; the fibres in each half belong exclusively to the lateral eye of the corresponding side. × 400.


18
cta.
hdrm.
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COPEPODA.

PLATE III.

Pontella.

Figs. 20–29. A complete series of ten consecutive sections through the right and left retinas in planes parallel to the horizontal plane of the animal. The sections are viewed from their dorsal faces. Figure 20 represents the most ventral section; Figure 29, the most dorsal. The plane of Figure 25 is approximately indicated by the incomplete dotted line *mu. con.* in Figure 18 (Plate II.). In the sections on the present plate the different bodies in the left retina have been designated by appropriate letters and figures. The eight rhabdomeres have been indicated simply by numbers; the same number always refers to the same rhabdomere. For the sake of distinction, the two cone cells have been marked *cl. con. 1* and *cl. con. 2*. Some of the nerve fibres (*n. fbr. 7* and *n. fbr. 8*) have been numbered in reference to the particular rhabdomeres with which they are associated. × 400.

25
n.fbr 7
cl.con 2
nl.con
cl.con.1
nl.rtn'
6
n.fbr
24
n.fbr 7
nl.rtn'
6
n.fbr 7
23
22
2
1
3 4 5
21
3 a
nl.hdrm
s
2
1
d.r
3 4 p
20
29
hdrm
cta
8
n.fbr 8
n.fbr 7
ins
n.opt
28
8
nl.rtn'
n.fbr 8
n.fbr 7
n.fbr
n.fbr 8
27
7
nl.con
cl.con
n.fbr 7
n.fbr
n.fbr 7
n.fbr 8
26
7
nl.rtn'
cl.con
nl.rtn'
6
n.fbr.

PONTELLA.

PLATE IV.

Branchipus.

(Figs. 30–32.)

Fig. 30. A longitudinal section of an ommatidium. × 400

" 31. A transverse section through the distal end of four cones. × 400.

" 32. A transverse section through the middle portion of a retinula. × 400.

Limnadia.

(Figs. 33–39.)

Fig. 33. A section through the anterior part of the body, including the eye, in a plane transverse to the chief axis. × 25.

" 34. An enlarged portion of a section from the same series as that from which Figure 33 was drawn, but in a position slightly anterior to the latter. × 115.

" 35. A section through the eye cut in the sagittal plane of the animal. Depigmented. × 90.

" 36. A lateral view of an ommatidium. The numbers at the left of the figure correspond to the numbers of the three following figures of transverse sections, and mark the levels at which the latter were taken. × 475.

" 37. A transverse section through the corneal hypodermis and distal ends of the cones. × 475.

" 38. A transverse section through four cones at the level where they are thickest. × 475.

" 39. A transverse section through the central portion of four retinulæ. × 475.

Evadne.

(Figs. 40–45.)

Fig. 40. An optical section through the eye and adjoining structures in a plane approximately parallel to the sagittal plane of the body, but lying somewhat to the right of it. × 140.

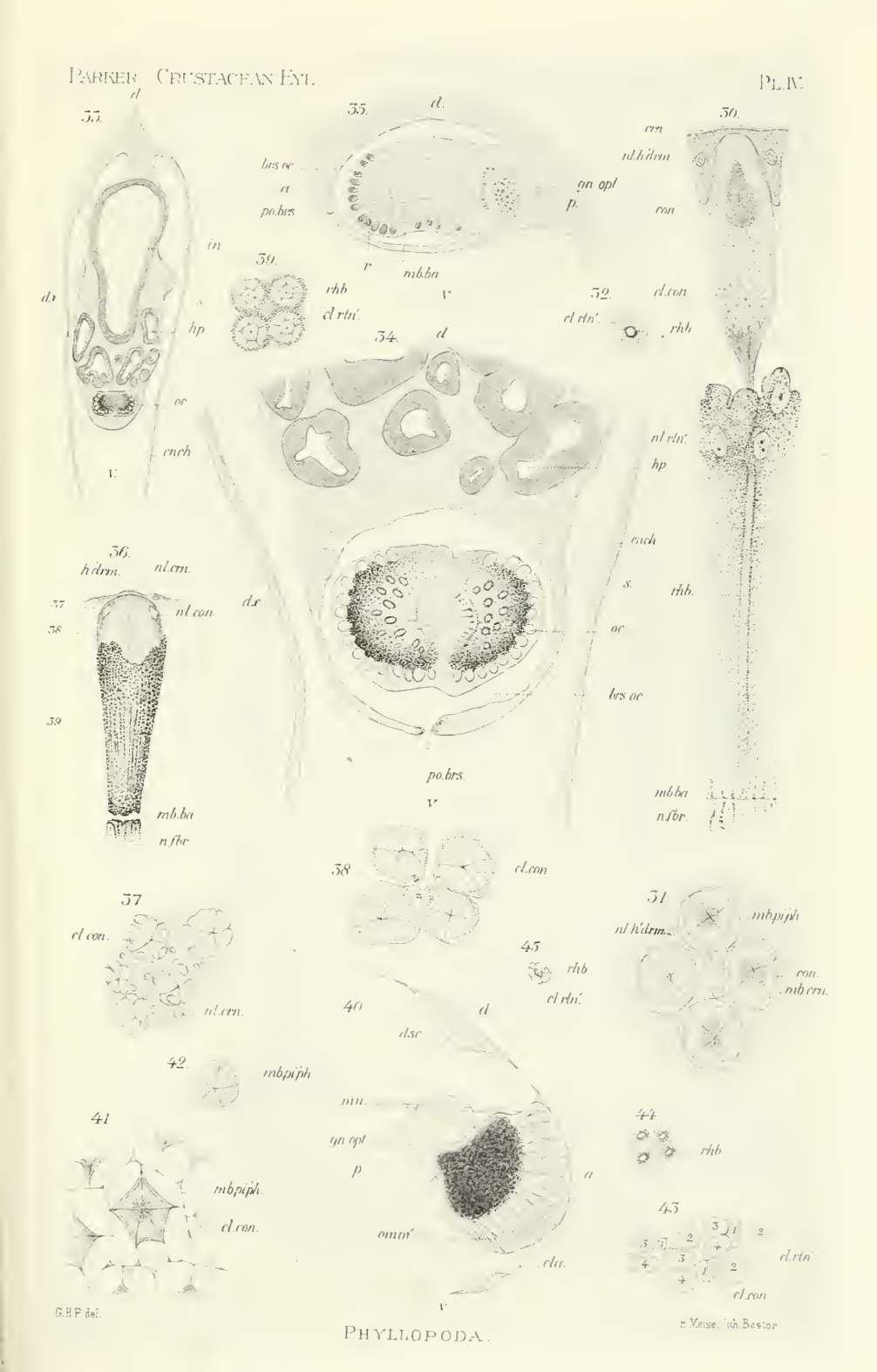
" 41. A transverse section through the distal ends of the cones. × 475.

" 42. A transverse section through the proximal end of a cone. × 475.

" 43. A transverse section through the distal ends of three groups of retinular cells. In each group the corresponding cells have been designated by the same number. × 475.

" 44. A transverse section through the central part of four rhabdomes. × 475.

" 45. A transverse section through a retinula. Depigmented. Kleinenberg's alum-hæmatoxylin. × 475.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E. Weise, lith. Bostor
PHYLLOPODA.

PLATE V.

Porcellio.

Fig. 46. A transverse section through a retinula in a plane slightly distal to the basement membrane. The single, light, central spot represents the proximal end of the rhabdome. × 475.

Idotea robusta, Kroyer.

(Figs. 47, 48.)

Fig. 47. A transverse section through the distal end of a retinula. The bodies, one of which is marked *x*, are spheres of coagulated material which occur in the interommatidial spaces, and which have been brought into prominence by the action of the hardening reagent. × 475.

" 48. A transverse section through three ommatidia in the region of their rhabdomes. × 475.

Idotea irrorata, M. Edws.

(Figs. 49–57.)

Fig. 49. The anterior face of a section transverse to the chief axis of the body, and passing through the eye on the right side of the head. × 140.

" 50. A longitudinal section of an ommatidium. The numbers at the left of the figure correspond to the numbers of the following six figures of transverse sections and mark the levels at which the latter were taken. × 475.

" 51. A transverse section through the distal ends of the cones. × 475.

" 52. A transverse section through the middle region of a cone. × 475.

" 53. A transverse section through the middle of a retinula. Near the centre of each cell can be seen a small axis of nerve fibrillæ. × 475.

" 54. A transverse section through a retinula composed of seven cells instead of six. This section was cut approximately at the same level as that shown in the preceding figure. × 475.

" 55. A transverse section through a retinula near its proximal end. Each fibrillar axis is much larger at this plane than in that shown in Figure 53. × 475.

" 56. A transverse section of several groups of retinular cells immediately proximal to the basement membrane. × 475.

" 57. A transverse section of four retinular cells at the level in which their nuclei occur. The axis of nerve fibrillæ in the plane of this section and in that of the preceding one (Fig. 56) are smaller than they are at the base of the retina (compare Fig. 55).

Sphæroma.

(Figs. 58, 59.)

Fig. 58. A transverse section of a retinula at a level slightly distal to the basement membrane. × 475.

" 59. A transverse section of the fibrous ends of the cells from a single retinula. The plane of section is slightly proximal to the basement membrane. The only indication of an axis of nerve fibrillæ is the more transparent condition of the central part of the cells, due to the partial absence of pigment granules. × 475.

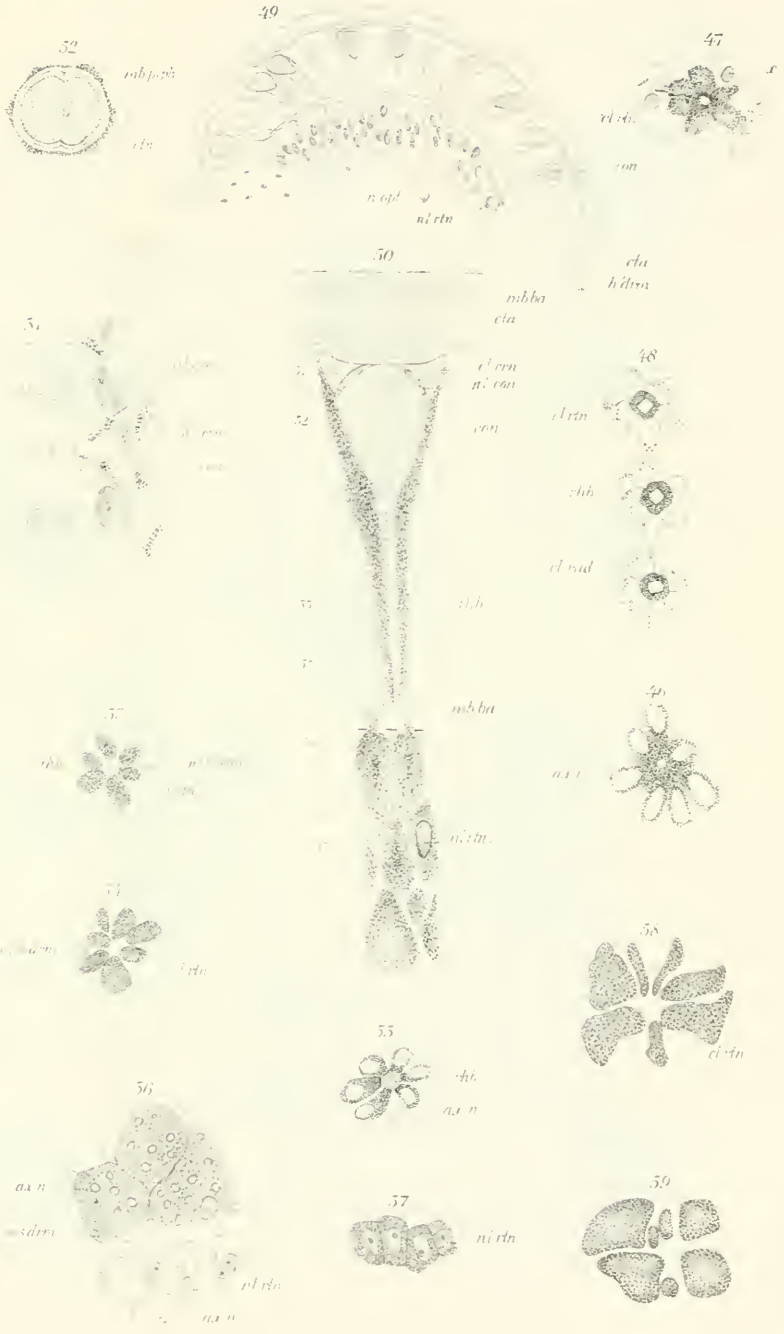
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PLATE VI.

Serolis.

Figures 60 to 64 inclusive represent the structure of the ommatidium in the adult. Figures 65 to 72 are drawn from sections of ommatidia in well advanced embryos. All figures are magnified 475 diameters.

Fig. 60. A tangential section through the most distal portion of the retina. This section includes a portion of a cone and the tissue lying between it and two adjoining cones.

" 61. A transverse section of a retinula in the region of its rhabdome. The arrangement of the pigment granules and nerve fibrillæ is indicated in only one of the four cells. Of the two lines which appear to separate the cone cells (*cl. con.*) from the rhabdomere (*rhb'm.*), the one nearer the axis of the ommatidium is the real line of separation; the other lies within the substance of the rhabdomere itself (compare p. 92).

" 62. A transverse section through a retinula proximal to the rhabdome and in the region of the hyaline cell. As in Figure 61, the pigment granules are drawn in only one of the retinular cells.

" 63. A transverse section through a single retinular cell in the region of its nucleus. The axis of nerve fibrillæ is represented by several small axes in the substance of the cell at one side of the nucleus.

" 64. A transverse section of the fibrous ends of the cells of one retinula in their passage through the aperture in the basement membrane. Each cell shows a well marked fibrillar axis, the centre of which is often occupied by a core of pigment. The basement membrane is viewed from its distal face. The irregularly oval body in the upper left-hand corner of the figure is probably a nucleus. It lies on the proximal face of the membrane through which it is seen.

" 65. A longitudinal section through the ommatidium of an advanced embryo. The numbers at the left of the figure correspond to the numbers of the six following figures of transverse sections, and indicate the levels at which the latter were taken. Figure 68 represents a section so nearly in the same plane as that shown in Figure 67 that its number has been omitted.

" 66. A transverse section at the level of the corneal hypodermis.

" 67. A transverse section through the distal end of a cone.

" 68. A transverse section made in a plane only slightly proximal to that shown in Figure 67.

" 69. A transverse section through the region of the distal retinular nuclei.

" 70. A transverse section through the proximal ends of the cones.

" 71. A transverse section through the retinula in the region of the rhabdome.

" 72. A transverse section at the level of the proximal retinular nuclei.

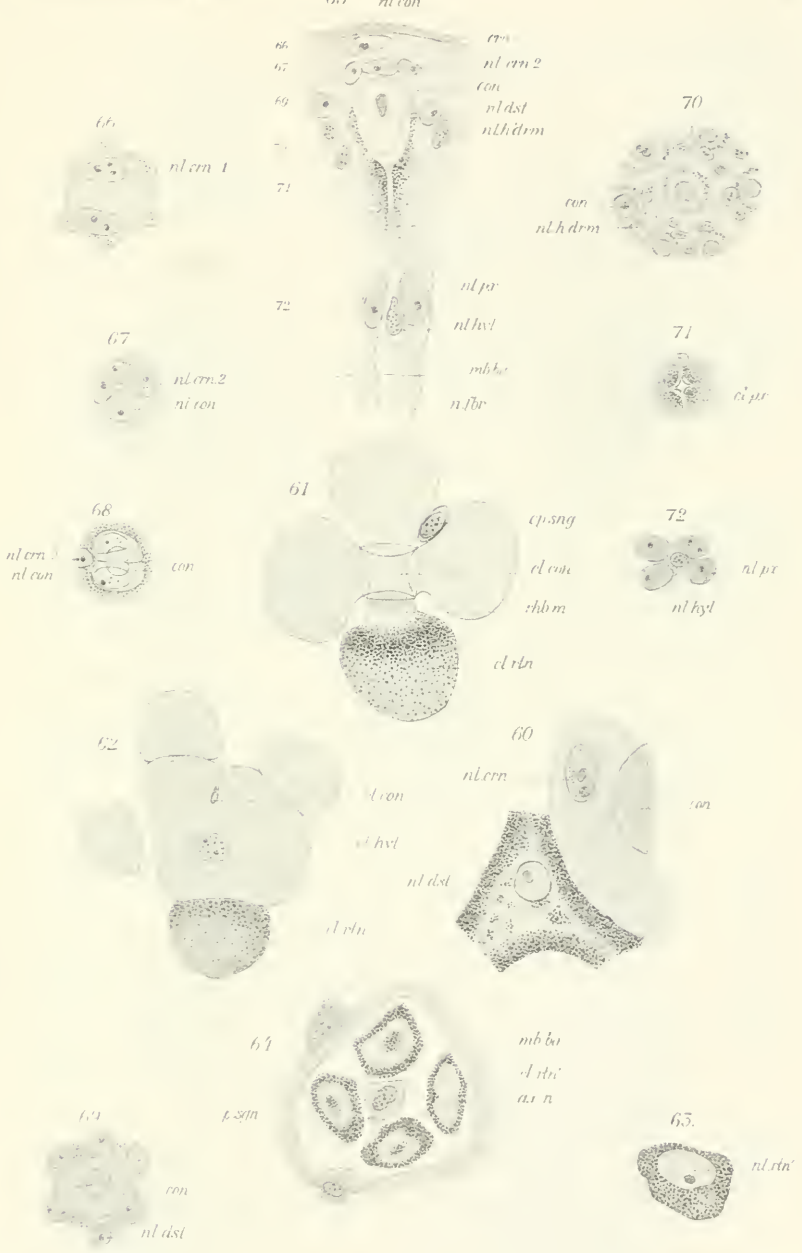
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PLATE VII.

Mysis.

Fig. 73. A longitudinal section of an ommatidium. The numbers at the left of the figure indicate the levels at which the sections for Figures 75–89 were taken. × 475.

" 74. The distal face of a corneal facet, cleaned in potash and examined in water. × 475.

" 75. A transverse section of three ommatidia in the plane of the corneal hypodermis. × 475.

" 76. A transverse section through the distal end of a cone. × 475.

" 77. A transverse section through the proximal end of a cone and the adjoining distal retinular cells. × 475.

" 78. A transverse section similar to that shown in the preceding figure, except that it is depigmented and stained in Kleinenberg's alum-hæmatoxylin. × 475.

Figures 79 to 82 inclusive represent consecutive transverse sections through the region of the proximal retinular nuclei of four adjacent ommatidia. The centre of each ommatidium is indicated by the group of cone cells (*cl. con.*), and the corresponding ommatidia in different sections are designated by the same Roman numeral. The nuclei around ommatidium II. have been numbered in Figures 79–81. Figure 79 represents the most distal section, and Figure 82 the most proximal one of the series.

Fig. 79. The bodies marked *x* and *y* are portions of nuclei the rest of which are correspondingly marked in Figure 80. × 475.

" 83. A transverse section of the four fibres at the distal end of the rod (compare p. 102). Depigmented, and stained in Kleinenberg's alum-hæmatoxylin. × 615.

" 84. A transverse section of the rod at a slightly more proximal level than that shown in Figure 83. Depigmented, and stained in Kleinenberg's alum-hæmatoxylin. × 615.

" 85. A transverse section of the retinula somewhat distal to the distal end of the rhabdome (compare Fig. 90). Depigmented, and stained in Kleinenberg's alum-hæmatoxylin. × 615.

" 86. A transverse section from the region between the distal end of the rhabdome and the proximal end of the rod (compare 86 in Fig. 90). Depigmented, and stained in Kleinenberg's alum-hæmatoxylin. × 615.

" 87. A transverse section through the rhabdome and surrounding retinular cells. × 615.

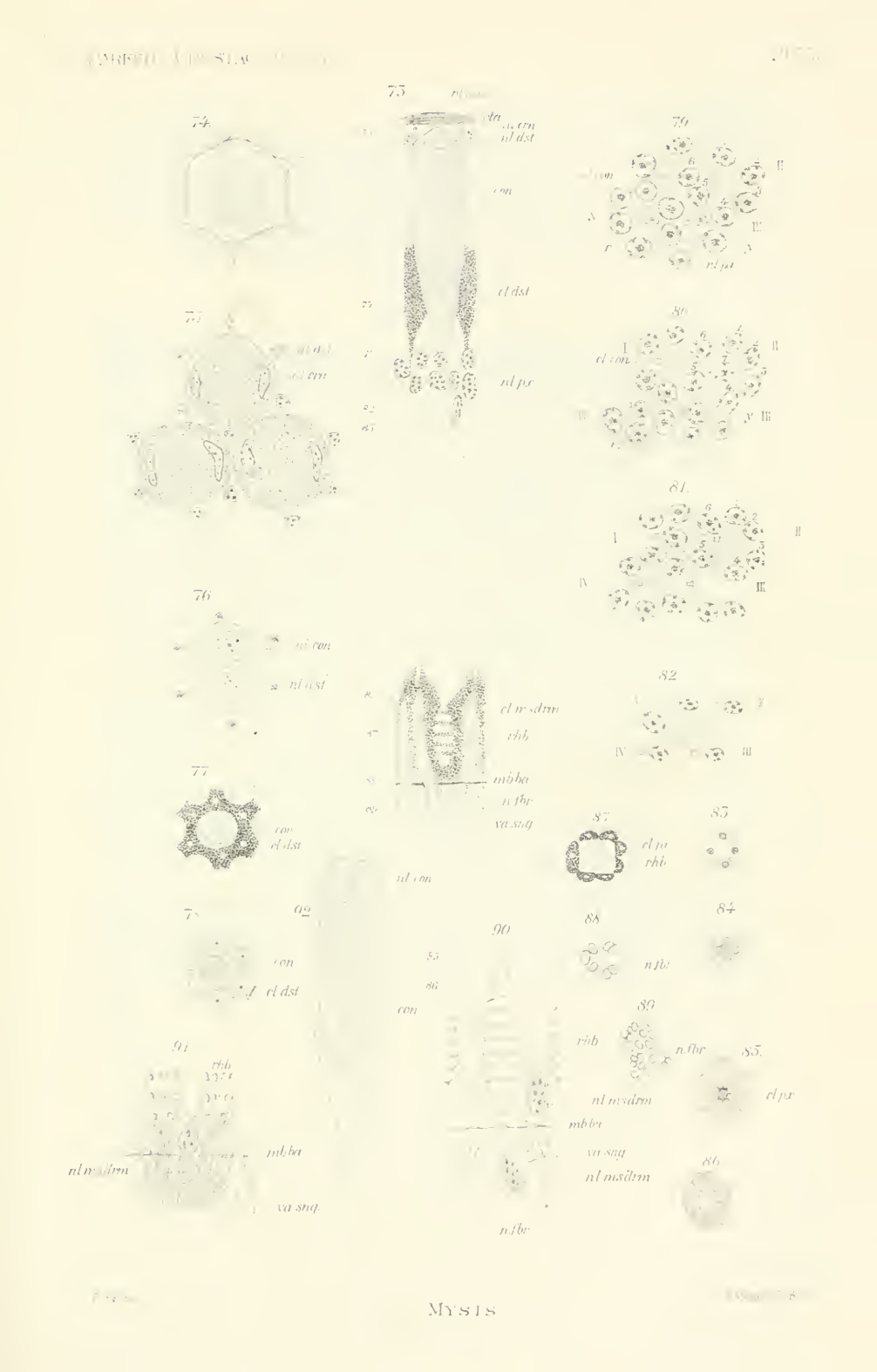
" 88. A transverse section, at the level of the basement membrane, through the nerve fibres from a single retinula. Depigmented, and stained in Weigert's hæmatoxylin. × 615.

" 89. A transverse section through the fibres of the optic nerve at a level midway between retina and optic ganglion. Preparation as in Figure 88. × 615.

" 90. A longitudinal section through the basal portion of one and parts of two adjoining ommatidia. Depigmented, and stained in Kleinenberg's alum-hæmatoxylin. × 615.

" 91. A section cut in the same plane as that shown in the previous figure, but including only the proximal ends of two rhabdomes. Preparation as in Figure 90. × 615.

" 92. A cone viewed from the side. Isolated in Müller's fluid and studied in water. × 475.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Mysis

PLATE VIII.

Gonodactylus.

Fig. 93. Part of a tangential section through a superficial portion of the retina. The extreme edges of the section both right and left are immediately beneath the corneal cuticula; the central portion is farthest from the cuticula. At the right of the middle line are seen the ends of the larger ommatidia; at the left, those of the smaller. × 275.

" 94. A longitudinal section of a large ommatidium. The numbers at the left of the figure correspond to the numbers of six figures of transverse sections (Figs. 96–101), and mark the levels at which the latter were made. Depigmented. × 275.

" 95. A longitudinal section of a small ommatidium containing its natural pigment. × 275.

" 96. A transverse section through the cells of the corneal hypodermis and the distal end of the cone in a large ommatidium. × 275.

" 97. A transverse section through the distal part of a cone in a large ommatidium. × 275.

" 98. A transverse section through the middle of a cone from a large ommatidium. × 275.

" 99. A tranverse section through a number of cones at the level of the distal retinular nuclei in the large ommatidia. × 275.

" 100. A transverse section through six retinulæ of the large ommatidia in the region of the proximal nuclei. Each retinula is numbered. The plane of this section is slightly oblique, so that retinula 1 is cut at a relatively higher level than any of the others, and retinula 6 at the lowest level. × 475.

" 101. A transverse section of a retinula from one of the larger ommatidia, in a plane not far from the basement membrane. Depigmented. × 475.

" 102. A transverse section of a retinula from one of the smaller ommatidia cut in a plane nearly corresponding to that of Figure 101. × 475.

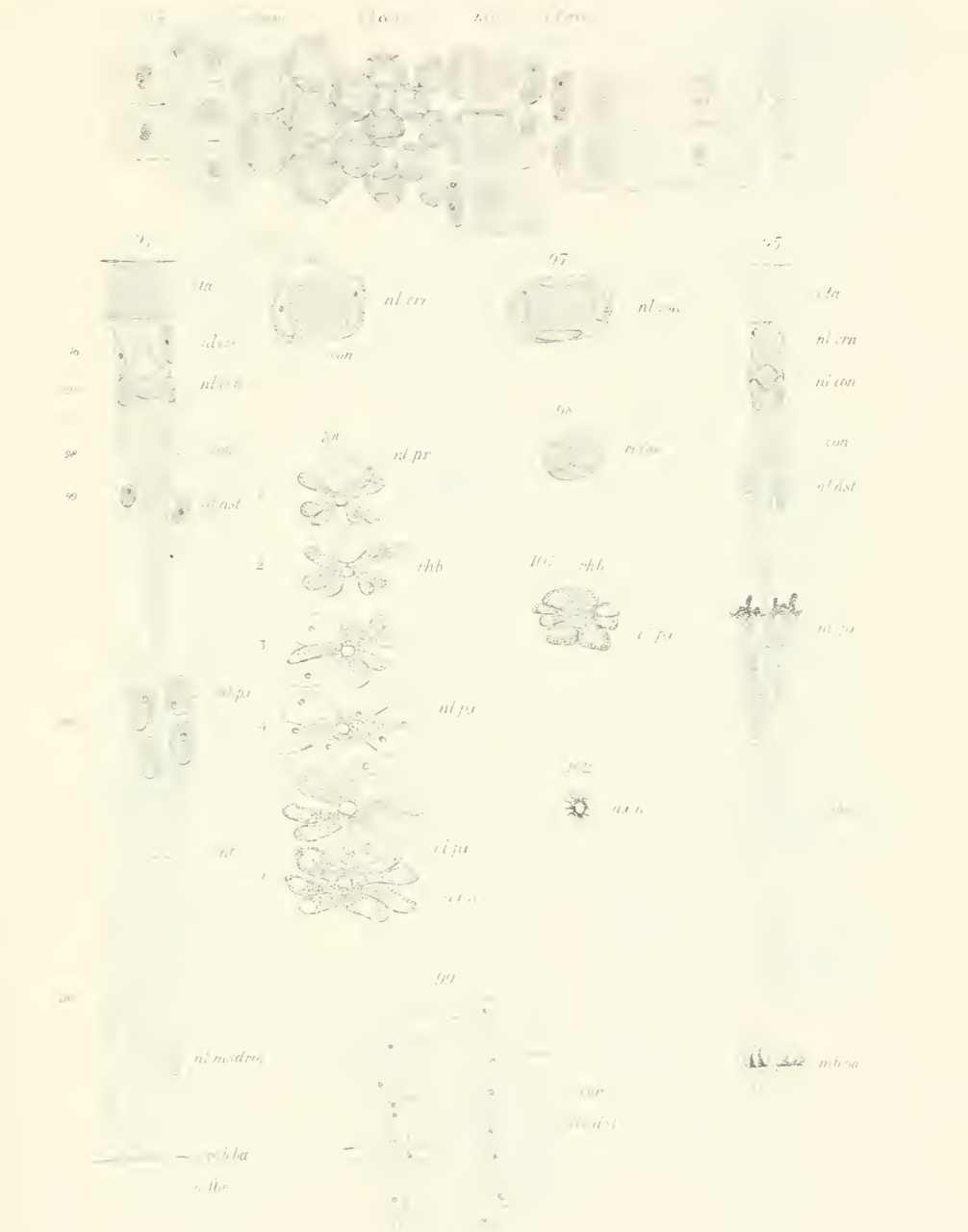
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PLATE IX.

Palæmonetes.

In all Figures on this plate the magnification is 475 diameters.

Fig. 103. A longitudinal section of an ommatidium. The numbers at the left of the figure correspond to the numbers of nine of the following figures of transverse sections, and mark the levels at which the latter were taken.

" 104. A longitudinal section of an ommatidium which has been depigmented. The bodies marked *x* resulted from the action of the depigmenting reagent.

" 105. A facet from the corneal cuticula; cleaned in strong potassic hydrate, and examined from its distal side in water.

" 106. A transverse section through the region of the corneal hypodermis.

" 107. A transverse section through the distal end of a cone in the region of the nuclei of the cone cells.

" 108. A transverse section through the middle of a cone.

" 109. A transverse section through parts of four ommatidia in the region of the distal retinular nuclei.

Figures 110–112 represent three successive transverse sections, each through five ommatidia, in the region of their proximal retinular nuclei. Only the outlines of the nuclei and the five groups of cone cells (*cl. con.*) are drawn. The nuclei in each ommatidium are numbered from 1 to 7, and as their plan of arrangement is the same in the different ommatidia, corresponding nuclei have been designated by the same number. In some cases the nuclei were cut in two, and consequently appear in two adjoining sections. In such cases the two parts have been marked with the same number. Figure 110 is the most distal of the series; Figure 112, the most proximal.

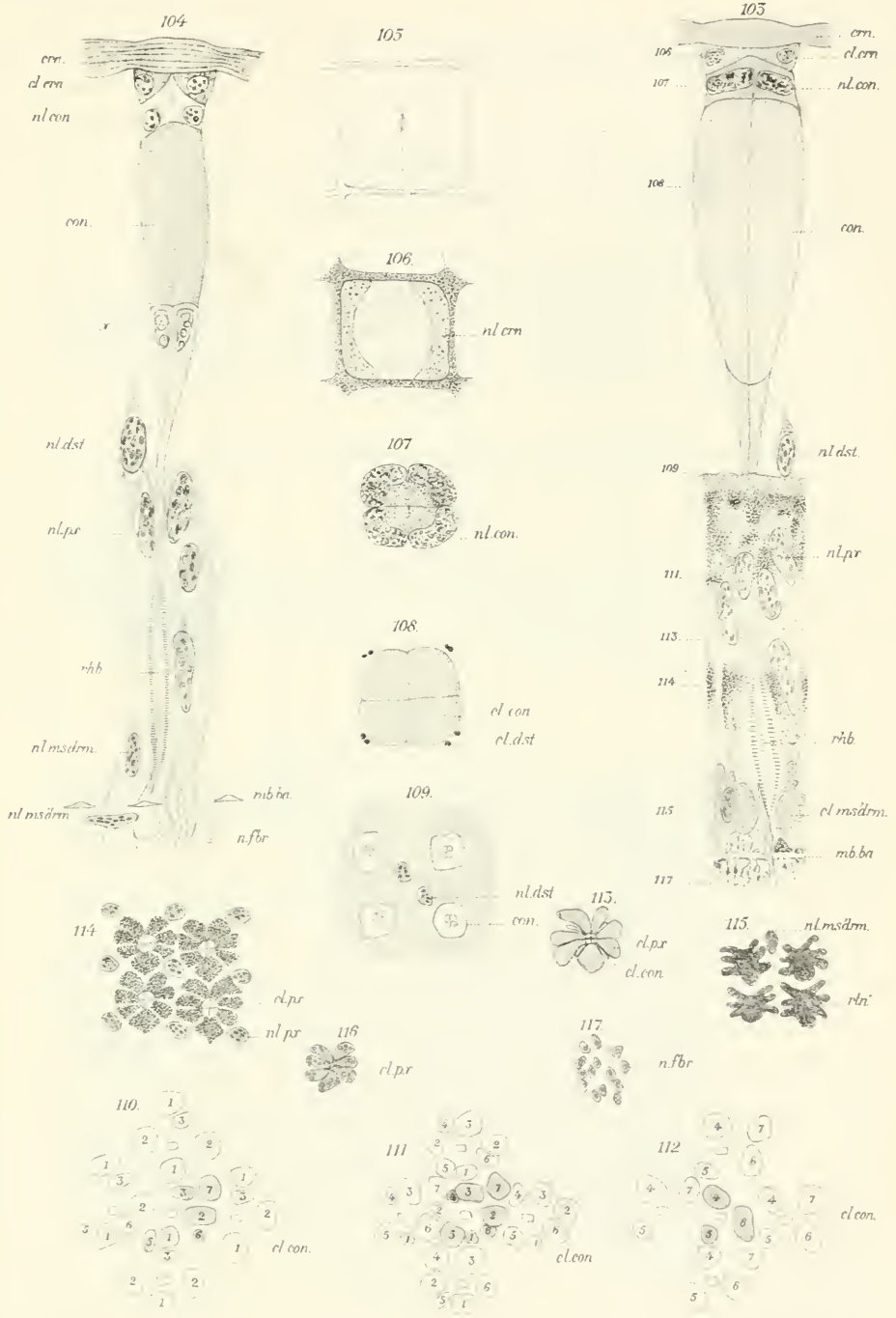
Fig. 113. A transverse section of the retinula near the distal end of the rhabdome. Depigmented.

" 114. A transverse section of four retinulæ at the level of the eighth retinular nucleus.

" 115. A transverse section through four retinulæ in the region of the accessory pigment cells; viewed by *reflected* light. The retinulæ appear as dark masses embedded in a whitish field composed for the most part of the substance of the accessory pigment cells.

" 116. A transverse section through a retinula at about the same level as that shown in Figure 115. Depigmented.

" 117. A transverse section through the optic nerve fibres at a level slightly proximal to the basement membrane. Depigmented.



PALÆMONETES.

PLATE X.

In all Figures on this plate the magnification is 475 diameters.

Cambarus.

Figures 118–122 represent a series of five successive transverse sections through one and parts of four adjoining ommatidia in the region of their proximal retinular nuclei. Figure 118 represents the most distal section in the series, Figure 122, the most proximal. In these figures, only the outlines of the nuclei and the groups of cone cells are drawn.

Crangon.

Fig. 123. A transverse section through a number of ommatidia in the region of their distal retinular nuclei.

Palinurus.

Fig. 124. A transverse section through a retinula in its middle region. The outlines of the retinular cells cannot be distinguished; the position of each cell is marked by an irregular light mass in its centre.

" 125. A transverse section through a retinula in the plane of its eighth nucleus. Depigmented.

Cancer.

(Figs. 126–131.)

Fig. 126. A corneal facet viewed from its distal surface. The cuticula from which this facet was drawn was cleaned by being boiled in a strong aqueous solution of potassic hydrate. It was examined in water

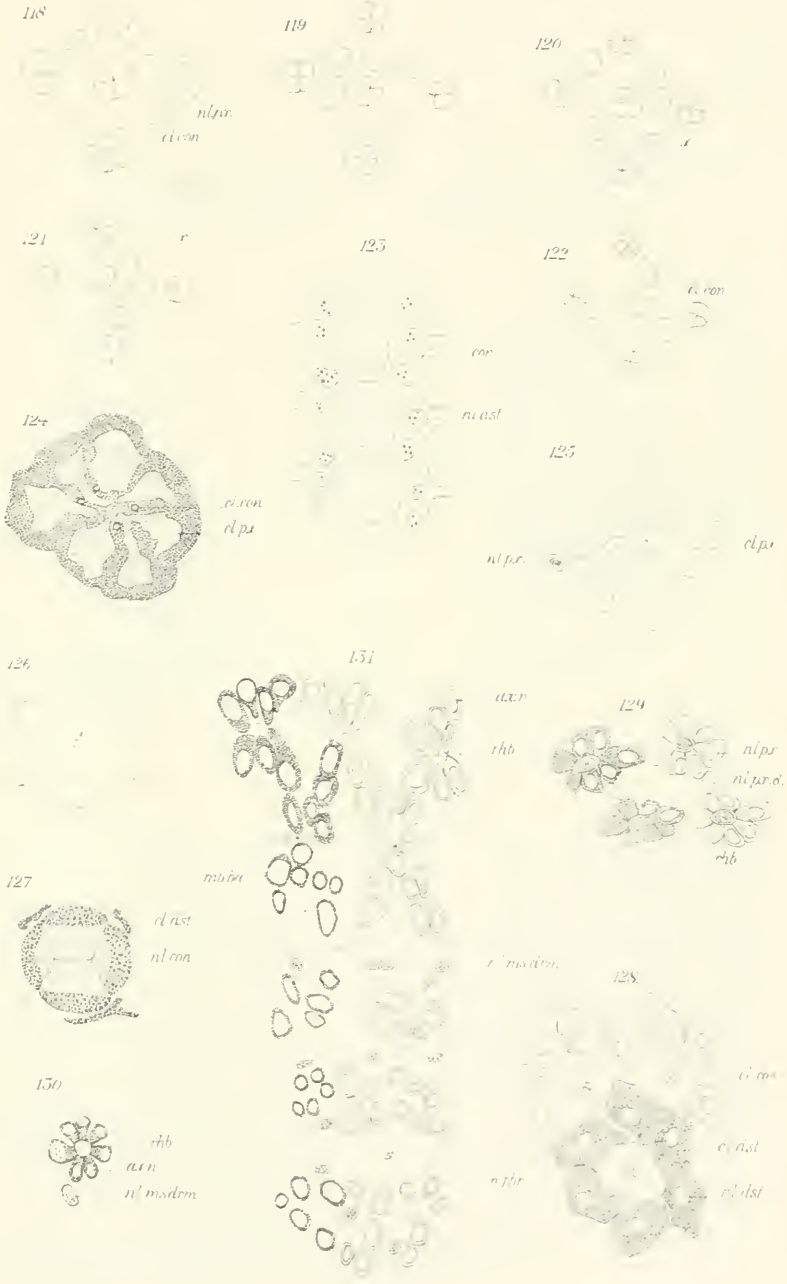
" 127. A transverse section of the distal end of a cone.

" 128. A transverse section through three ommatidia at the level of the distal retinular nuclei. The pigment granules have been indicated in only the lower circle of cells.

" 129. A transverse section through the distal region of four retinulæ. In the two on the right, the pigment granules have not been drawn

" 130. A transverse section through a retinula near the base of the retina.

" 131. A slightly oblique section through the basement membrane. The upper part of the figure represents the retinulæ as seen in transverse section distal to the basement membrane; the part marked *mb. ba.* represents the region in which the membrane itself appears in section, and the lower half of the figure shows the cut fibres of the optic nerve. The pigment granules are omitted from the right side of the figure. The transition from the retinular cells to the nerve fibres is evident in passing over the section from top to bottom.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No. 3. — *On some Points in the Anatomy and Histology of Sipunculus nudus*, L. By Henry B. Ward.[1]

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I. Introduction.

Some two years ago, while working on Sipunculus nudus in the zoölogical laboratory at Göttingen under Prof. E. Ehlers, my attention was attracted by a peculiar organ in the region of the dorsal ganglion; and although it was a prominent feature of all transverse sections, no mention of its presence was found in the literature on Sipunculus. The observations made at that time interested me so much that the opportunity afforded by a short stay at the Naples Zoölogical Station last spring, for which I am indebted to the great kindness of Prof. A. Weismann and the Cultusministerium of Baden, was embraced to procure new, carefully preserved material. A study of the literature on Sipunculus revealed such lack of agreement between authors that a more general study of the form seemed likely to yield results, and, on the advice of Prof.

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXVI.

E. L. Mark, a more particular consideration of some moot anatomical and histological points was undertaken. This was unfortunately limited by the material on hand, which consisted merely of the anterior portion of the body, corresponding in general to the introvert of recent writers. As this contains, however, nearly all of the important organs of the nervous system to which especial attention has been paid in this paper, and as its separation from the rest of the body at the time of killing insured good preservation, it is hoped that the conclusions reached may not be without value, in spite of their incompleteness. The histological structure of the body wall and of the nervous system has been treated in detail, and from the results an attempt has been made to throw some new light on the systematic position of the Sipunculids.

Methods.

The material used in these investigations was preserved with especial care, and every effort was made to procure a method of killing which should afford a clear idea of anatomical and histological relations under normal conditions, since many of the contradictory statements of various writers have been undoubtedly the result of studying specimens in a distorted state, due to muscular contraction, or have followed the examination of tissues poorly preserved. The thick impermeable cuticula, and the wealth of muscular tissue in the body wall, render it a difficult matter to avoid at the same time both evils. The method finally adopted as yielding the best results is as follows.

After remaining some time in clean sea-water to clear tentacles, body wall, and œsophagus of adhering sand, the animals were brought into a shallow dish of sea-water, and 5% alcohol was allowed to flow gently over the surface, forming thus a thin film, which disseminated itself gradually, and produced in the animals a complete relaxation of the body muscles. It did not seem to answer equally well when the alcohol and water were mixed at the start, as has been recommended for some animals. The length of time necessary for the attainment of complete narcosis cannot be exactly given. It varies greatly with different individuals; but if, after lying some four to eight hours, the animals make no contractions on being gently probed with a dull instrument, they may be regarded as sufficiently stupefied, and transferred to 50% alcohol. After a short stay in this, the introvert was cut off, and this alone subjected to treatment with higher grades of alcohol, which insured the penetration and consequent good preservation of the tissues. The only point in the process which requires especial care, and which often produces

a disappointing failure, is the transfer from the salt water and its added alcohol to 50% alcohol. If the animal is but partially narcotized, the muscular contraction induced by the transfer will spoil the specimen. If, on the other hand, it be left too long, the weaker parts of the body wall, especially the upper smooth zone of the introvert, swell out quite rapidly (through osmosis?), and not only the external form but the histological elements as well are badly distorted. The golden mean between these two extremes yields specimens as excellent for histological work as for the study of external relations. Material preserved in this way may be well stained by all methods. Where any stain has been of especial value in the study of particular organs or tissues, it will be noted under the topic in question. In this place I wish to express my thanks to Prof. E. Ehlers of Göttingen and to Prof. A. Dohrn of Naples for past favors, and to Mr. A. Agassiz, Prof. E. L. Mark, and Prof. E. B. Wilson for more recent kindnesses in supplying me with material for this study.

II. External Anatomy.

Selenka ('83, p. 92) has given a full description of the external characters of *Sipunculus nudus*. There are however numerous points of interest which first appear in a well expanded specimen, and which deserve especial attention. The body consists of a large posterior region covered by the quadratic integumentary areas (Hautfelder) and of a portion anterior to these, which is called the introvert.

1. Introvert.

This includes on the average one sixth of the entire length of the animal, and has in general the shape of a truncated cone (Fig. 1), the anterior base of which, only a little less in diameter than the posterior, is surmounted by a wreath of tentacles which nearly encircle the mouth. This region is ordinarily found entirely, or for at least two thirds of its length, invaginated into the following portion of the body, and is only rarely seen extended. In the latter condition it measures from three to four centimeters in length. The circular muscle bands, which are separate in the posterior part of the body, are here fused into an unbroken sheet of muscular tissue. The fusion takes place abruptly, and causes the immediate cessation of the integumentary areas (Hautfelder) due to the banded musculature, thus fixing a definite posterior boundary to the introvert. On the latter one can distinguish (Fig. 1) four regions:

(1) a posterior papillate zone [1] (*z. pap. p.*), (2) a smooth zone (*z. lev.*), (3) an anterior papillate zone (*z. pap. a.*), and (4) the tentacular crown (*pli. ta.*).

The posterior papillate zone occupies the posterior half of the introvert, and shows a posterior portion, which is thickly studded with papillæ, and is dark brown in alcoholic specimens, and an anterior part much lighter in color, where the papillæ are somewhat scattered. The lighter, almost translucent appearance of the anterior portion of this zone, which permits the central mass of the œsophagus and retractors to shine through as a dark band, is due to the great diminution in thickness of the muscular layers. The line of demarcation between the lighter and darker portions of this zone is somewhat definite, and is marked internally by the fusion of the longitudinal muscles into a continuous sheet, and by the entrance into the body wall of the first large composite nerve given off from the ventral nerve cord (*cf. infra*).

The papillæ of this region are all shaped like the bowl of a spoon with the concavity directed toward the body and the tip posteriad. Adjacent to the integumentary areas they are closely crowded, and overlap like the shingles of a roof, so as to hide the skin completely. They vary in size and shape, but are in general broadly pointed, measuring on the average .25 mm. in length, and .65 mm. in breadth.[1] Passing forward, this general form is preserved until the point of transition from the dark to the light portion of this posterior papillate zone is reached. Here the papillæ grow abruptly smaller in absolute size, though relatively longer and narrower, until the characteristic mammiform papilla of the light region is reached. These only are represented in Figure 1. They are much lighter in color, and much less crowded, than the posterior papillæ, and leave irregular patches of skin entirely free. In breadth such a papilla measures .25 mm.; in length, .37 mm. I am unable to confirm the statement of Andreae ('81, p. 205), that they are arranged "in gleichen Abständen"; for the relative distances are extremely variable, being from 70 to 300 μ in the anterior portion of this zone. I was also unable to find the arrangement in a double spiral reported by Vogt und Yung ('88, p. 381). There seemed to be in fact no regular arrangement common even to a majority of the specimens examined.

Passing forward, the papillæ grow ever sparser, and finally terminate along a well defined line, which marks the beginning of a smooth zone (*z. lev.*, Fig. 1) entirely free from papillæ. It measured 7 mm. in breadth in a specimen which had an introvert of 4 cm. total length. Anterior to

[1] The posterior half of the posterior papillate zone is not shown in Figure 1.

this is a zone (*z. pap. a.*) with small papillæ; this measured 3 mm. in breadth in the same specimen. The papillæ of this zone appear superficially as minute discoidal elevations of the skin. In well expanded specimens, the tentacles droop over and nearly cover this zone, which is not separated from their base by any definite line, since the papillæ extend forward a short distance over the aboral surface of the tentacles, becoming gradually less frequent. They are indeed met with occasionally on the whole of this surface, but are entirely wanting on the oral aspect of the tentacles. In all well expanded specimens these regions are as well defined as in the one which has served as the basis for this description, and the zones have the same relative size as in the measurements given.

2. Tentacular Fold.

The tentacles (Tentakelmembran) originate in the larva as two folds of the oral margin, — "lippenartige Falten," Hatschek ('83, p. 115), — separated dorsally but continuous ventrally, and lying right and left of the median line. Starting, then, from this primitive condition, the form found in the adult would be reached, if it be supposed that these flaps of skin are plaited radially to the oral centre, and that the growth is more rapid on the oral surface as well as toward the margin, thus necessitating a reflection of the flaps back upon the aboral surface. For a careful examination shows that in well expanded specimens the so-called tentacles consist of a thick fold of skin surrounding the terminal oral orifice with numerous plaits and folds arranged radially. This continuous flap may be called the tentacular fold, in preference to membrane, since the latter suggests a false idea of its nature, and its subdivisions may conveniently be termed the radial plaits.

The general form of the tentacular fold, as viewed from above (Fig. 2), may be said to be that of a horseshoe with the smaller dorsal curvature interrupted on the middle line. The external or ventral semi-circumference is reflected over the superior portion of the introvert, whereas the internal or dorsal portion makes a ventral flexion over the mouth, and lies higher than the other half of the tentacular fold. The superior height of the dorsal portion of the flaps in the larva caused Hatschek ('83, p. 115) to regard this as the "Anlage" of the first pair of tentacles. He knew nothing, however, of the further development of this portion, which probably represents the origin of the dorsal horns, since separate tentacles do not exist. In the adult, at any rate, this region shows two horns (Figs. 1 and 2, *crnu. d.*) projecting ventrad over the oral aperture, and

forming together the dorsal curve of the horseshoe. Brandt ('70, p. 22) assigned a horseshoe shape to the crown of tentacles, but this has been declared false by later investigators.

This normal hippocrepian form is often distorted when the introvert is only partially extruded, or when there is undue muscular contraction within the soft mass of the fold itself, and it is always more or less disguised by the secondary radial plaits into which the fold is thrown. The relation of these parts will be easily understood by comparing Figures 1, 2, and 3. It will thus be seen that the reflection of the tentacular fold, with its deep radial plaits, brings into prominence regions — the "triangular tentacles" of some writers — which alternate with retreating portions, so as to impart to the margin the appearance of being cut or toothed, especially if the contraction of the muscular elements in this soft fold has drawn it somewhat out of shape. In fact, the description uniformly given by systematic writers has represented the tentacles as a membrane with numerous marginal incisions. This error is due in part to distorted specimens; the true form may be said to be crenate.

Therefore one can speak of the formation of tentacles only in a general sense. But the fold may be regarded perhaps as the simpler form, from which, by the development of certain areas alternating with regions of reduction, the more highly specialized digitate tentacles might be developed. Only the main folds are represented in Figure 2. These may be much complicated by the appearance of subordinate plaits, until the general plan is confused by a mass of detail. The more simple forms proved, on microscopic examination, to have been the most successfully killed, in that the muscular elements were in a more perfectly relaxed condition. The aboral surface of the tentacular fold is concave, except in the dorsal horns, where it is convex; it has the same radial folds as the oral surface with which it is approximately parallel. Numerous low circular ridges traverse the aboral surface, and bear in varying number the small papillæ already mentioned. These ridges are not regular in course or size, and evidently vary with the convexity of the tentacular fold. In the midst of these, on the dorsal median line, can be found on careful examination a small oval opening (Figs. 2, 3, *can. o. ceb.*). It is often so hidden in the ridges of the aboral surface as to make its discovery a matter of some difficulty. The opening measures about 1 by 0.5 mm., with its long axis transverse, and is surrounded by an evident marginal ridge. This is the opening of the canal of the cerebral organ, to be described later.

III. Histology.

1. Body Wall.

In the body wall may be found the following layers, beginning with the surface : (1) a cuticula, (2) a hypodermis, (3) a cutis, (4) the muscular system, covered internally by (5) a delicate peritoneal membrane.

a. Cuticula and Hypodermis.

The cuticula consists of a substance optically like chitin, but differing from this, as has often been pointed out, in being soluble in boiling KOH. It is further aberrant in the absence of cellulose, which has been shown by Ambronn ('90) to be characteristic of true chitin. Tests with chloriodide of zinc showed neither any trace of blue nor the subsequent pleochroismus described by that author for true chitin. This layer is undoubtedly the product of the underlying hypodermal cells, which are everywhere found in a single layer, and normally display a sac-like form, although, as mentioned by Vogt und Yung ('88, p. 383), they may by contraction or compression of the body wall be drawn out into the form of spindles. This has given rise, as they mention, to the erroneous interpretation of such groups of elongated cells as being sensory organs. In contradistinction to these authors, I do not find the proximal ends of these cells ordinarily continuous with fibres which extend to the muscular layer, and cannot agree with them in regarding the entire mass external to the muscles as one layer. For if one examines a transverse section of the body wall as seen in Figure 5, the majority of the hypodermal cells are seen to be clearly marked off from the underlying tissue by the cell wall. The fibres of this subjacent tissue, to be described later, often extend up to the bases of the hypodermal cells; but close examination in favorable regions shows the connection to be merely apparent. Often when these cells are crowded and distorted by near-lying glands, one is inclined to believe in an actual continuity of cell and fibre which cannot be demonstrated, and which, so far as I could find, is not present in less confused regions.

Lying partly in the hypoderm, but mostly below it, are the dermal bodies (Hautkörper), which are of three sorts. A description of these will be given in the account of the cutis, with which they are most closely associated. No further specialized cells of any kind were found, neither sensory cells nor peculiar nerve endings of any sort, and I am inclined to regard the claims of their presence as founded upon the ex-

amination of poorly preserved material. Several times it was observed that delicate filaments, branching from some nerve fibre of the skin, proceeded to the hypodermis and penetrated apparently undifferentiated cells; certainly the distal surface of these cells bore no sensory hair or bristle. But the exact manner of termination of the nerve filament remained in doubt.

b. Cutis.

In placing a cutis in the list of the layers of the body wall, I am not unaware that the two most recent publications on Sipunculus deny its presence. As already mentioned, Vogt und Yung ('88) regard the entire extra-muscular layer as hypodermal, while Andrews ('90) evidently discredits the existence of a cutis by omitting the name altogether. What, then, is the actual condition of affairs? In sections one finds (Figs. 4, 5) between the hypodermis and the muscular layers a mass of gelatinous tissue, traversed in all directions by fibres, and containing not only glands of various sorts, but nerve fibres and pigment cells as well. Thus, though varying greatly in thickness in different regions of the body, it may properly be regarded, in the light of the characters mentioned, as a true cutis. The principal part of this layer is the connective-tissue jelly, homogeneous in its consistency and forming the matrix in which the nerves and dermal bodies lie. It is traversed in all directions by a multitude of the finest connective-tissue fibrils, which anastomose but rarely. Occasionally a minute nucleus can be observed in the course of a fibre. Scattered nuclei of a larger size, connected with nerve fibres or amœboid cells, are not infrequent in this mass, and have been erroneously regarded as belonging to the connective tissue. Irregular amœboid cells with but one nucleus and of a different refractive index from the general mass are found, sometimes in considerable numbers, and are perhaps similar in nature to the leucocytes of the tentacles, to be described later.

c. Pigment Cells.

Besides these elements one finds multinuclear cells of irregular outline more or less filled with granules of a highly refractive character. These are the pigment cells, so characteristic of this group that they deserve special consideration. Andreae ('81, p. 209) has given almost the only description of these peculiar structures. He represents the pigment granules as closely packed in meshes of connective tissue on which nuclei may be observed. This appearance is no doubt due to poorly

preserved material; the true nature of the cells, as well as the process of deposition of the pigment, can clearly be understood from a section such as is shown in Figure 5. The cutis contains here a group of irregular amœboid (?) cells, distinguishable from the surrounding mass by their refractive power, and containing from five to many deeply stained nuclei 3 μ in diameter. The cells are all without any proper membrane, though often surrounded by an envelope of connective fibres, and enclose a varying number of highly refractive granules distinguished by indifference to any coloring matter but pieric acid, which they take up with great avidity. Their natural color by transmitted light is a greenish yellow; by reflected, however, a dull brown or yellow. That the process of formation is gradual becomes evident on the examination of a section like Figure 5. In some cells are seen only a few such granules, or they are confined to one part of the cell; and all stages are present from this up to a mass of closely packed granules in which neither cell plasma nor nuclei are visible. Even in such cells the nuclei could be demonstrated by prolonged staining and thin sectioning. The plasma of these cells shows at first some slight affinity for hæmatoxylin, which disappears as the granules become more crowded. In the first stages of deposition the granules are mere bright dots too small to be measured; in the more thickly crowded cells they have reached often twice or thrice the size of a nucleus, and alongside of these are also granules as minute as those of the earlier stage. Such cells are present not only in the cutis, but also in all other organs of the body. They are not always as numerous as shown in Figure 5; in the tentacles they are quite rare, whereas the nervous system contains especially large numbers in all its parts. Somewhat similar cells were found by Bürger ('90) in the nervous system of Nemertines. Wherever these cells are found in Sipunculus they display the same structure, except that elsewhere than in the cutis they are only found well filled with granules. Whether a migration actually takes place, as is suggested by their evidently amœboid character, I was unable to determine. It is to the presence of large numbers of these cells that the papillæ of the posterior zone and the walls of the cerebral canal owe their dark color. The pigment cells are present in much greater numbers in large than in small specimens, i. e. in older than in less mature ones. I can confirm the statement of Vogt und Yung ('88, p. 386) that fasting rapidly decreases their number. It is not a necessary conclusion that this is to be regarded as reserve material. For even waste may, under the pressure of failure in the food supply, be drawn into the system and worked over again.

d. Dermal Bodies.

Various opinions have been held by different authors as to the morphological value of the dermal bodies. Keferstein und Ehlers ('61) described them as glands, Leydig ('61) regarded them as sensory organs; but later writers have inclined to the former view. Andreae ('81) described three varieties of these organs, whereas Vogt und Yung ('88) made the claim that the sensory organs, Andreae's third variety, do not exist, and that all of the glands are merely modifications of one sort. As to the first statement, they are undoubtedly correct; but to the latter view I am unable to assent. The transition from one sort of gland to the other, though plausible from surface views such as given by those authors, is only apparent. For if one examines carefully prepared sections, the seeming similarity gives way to a well marked difference. Not one of the glands is actually unicellular, as claimed by Vogt und Yung, and the multicellular contain never less than five cells, which serves to separate them clearly from the other kind, which is always bicellular. Moreover, their behavior toward staining fluids is very different. For while the bicellular glands take up hæmatoxylin with such rapidity as to become almost black in a few seconds, the multicellular are but little affected by this reagent. Carmine solutions stain the two about equally, but bring out the nuclei, which are invisible in a hæmatoxylin stain. And, finally, the morphological elements of the two sorts are essentially different, as will be shown. The old classification of bicellular and multicellular glands will therefore be retained, and the structure of each will be examined more in detail.

The *bicellular glands*, when viewed, even in the living animal, directly from above, display a clear zone along the line of the partition wall between the cells. This is invisible if the gland be viewed from the side, or at a considerable angle, and gives rise to various images if the line of sight be more or less nearly perpendicular to the surface. As the papillæ which contain the glands have sloping sides, never exactly alike, it is easy to understand how views of the glands from many different directions may be had from a surface inspection, and how the various images may give the appearance of a series from the bicellular to the multicellular gland. If one examines, however, sections of the skin perpendicular to the surface (Figs. 4, 5), the bicellular glands appear at once as a distinct type. Ordinarily spherical, they may often be found mutually flattened where several lie closely pressed together. They vary in diameter from 40 to 50 μ, and present very different appearances

according to the stain employed. The greatest number of structural details are obtained from those lightly stained with hæmatoxylin. Sections thus stained are represented in Figures 6, 7, and 8. Though evidently differentiated hypodermal cells, they lie almost entirely in the cutis, enveloped by a delicate coat of connective tissue, in which can be found occasional flattened nuclei. The distal half of each cell is occupied in great part by a large vacuole, directly continuous with that of the adjoining cell. The space thus formed measures $12 \times 15 \times 25\ \mu$, and communicates with the exterior by means of a narrow canal opening simply on the surface of the cuticula. The duct measures $6–8\ \mu$ in diameter, and at the distal end of the cell does not lie in the centre of the neck (Fig. 9). The connective-tissue envelope does not penetrate between the cells, which in consequence are separated *only* by their own membranes (Fig. 6 or 11,*), and these, continued over or under the distal vacuole, appear, if the cell be viewed along the plane of the partition, to bisect the vacuole (Figs. 6, 10), the latter suffers, however, a slight constriction along this line, so as to impart to it in transverse section a biscuit-shaped appearance (Fig. 7). Its longitudinal section is cordiform, as shown in Figure 6. The two large clear spherical nuclei, $9\ \mu$ in diameter (Figs. 10, 11), may be differentiated with carmine or saffranin, and then appear in the lower half of the cell, usually nearly symmetrical to the dividing membrane. Each displays a single central deeply stained nucleolus, and many minute chromatine granules. If the plane of the section pass transversely *below* the vacuole (Fig. 11), the cells are seen to possess a hemispherical form, and the dividing membrane to make an S-shaped curve.

Whether active or resting, a clear zone of plasma forms the periphery of the cell on all sides, and is therefore adjacent to the vacuole, as well as to the external surface of the cell. This zone is traversed radially by delicate fibrils, the beginnings of the plasma reticulum which fills the cell, but which ordinarily is easily seen only in this clear zone. In every section one finds a few cells of this sort, which, besides an empty vacuole, exhibit this reticulum very plainly throughout the entire faintly tinted cell body (Fig. 8).[1] They are evidently the functionally inactive or resting cells. The first stage in secretion is seen in the accumulation of numerous granules in the basal portion of the cell (Fig. 6), which are stained deeply with hæmatoxylin, and by continual aggregation

[1] Strictly speaking, Figure 8 represents the *last* phase in secretion. The first differs only in the absence of matter in the vacuole, and of the few granules just below it.

finally obscure the reticulum, and impart to the entire cell, save its marginal zone, an appearance almost opaque (Fig. 7). The secretion first appears in the vacuole in the form of minute beads at the peripheral ends of the reticular fibrils which traverse the clear zone and terminate at the edge of the vacuole each in a single bead (Fig. 7). During the formation of the secretion in the vacuole, the mass of opaque granules moves toward this space; and the close of the process is represented in Figure 8, where the vacuole is filled with a homogeneous mass, displaying in a somewhat lesser degree the affinity for hæmatoxylin stains which characterized the granules while contained in the cell substance itself. At the same time, these granules have disappeared, except a few which are grouped in a zone about the vacuole; and the cell has become thereby so much lighter as to show the reticulum at its proximal end.

This description of the activity of these organs would seem to place their glandular nature beyond question. In comparing the two sorts of glands, it is of great importance to note that the cells do not show in this case any connection with nerves, whereby they are sharply distinguished from the multicellular glands. The space (Spalt) which Andreae ('81, p. 215) describes as existing between the cells of these glands was found not infrequently in some preparations, but it is evidently due to shrinkage. The double membrane separating the cells, described by the same author, was probably produced in the same way.

The distribution of these glands is peculiar. Over the general surface of the body they are found only rarely, and on the introvert they are present only *in the papillæ*, the interspaces being entirely free from them. Each papilla of the posterior zone of the introvert shows in surface views an irregular double or triple row crossing the convex outer surface near the base, and occupying one half to one third of its entire breadth. Rarely isolated bicellular glands are found near the tip. This regular limited distribution allows perhaps a conjecture as to their possible function. Inasmuch as the behavior of the secretion toward coloring reagents would seem to mark it as mucine (cf. Hoyer, '90), may it not be that these glands furnish the lubricant demanded by the constant movements of the two walls of the introvert? The papillæ are especially affected, of course, rubbing against each other in the constant inversion and eversion. They receive, furthermore, the greater part of the pressure as the animal forces its way through the sand, in the method described by Andrews ('90, p. 391). The animal does not advance backward with the "Eichel voran," as maintained by An-

dreae ('81, p. 220)! The secretion may also be of use in cementing the sand grains into a sort of tube noticeable when the animals are dug out of the sand.[1]

The *multicellular glands* present a type easily distinguishable from that just described. They are to be met with everywhere, not only in the papillæ, but lying in the interspaces as well, and extending up into the clear zone of the introvert, where they are the only differentiated hypodermal cells. Never much crowded, they become here sparser, until they completely disappear at the level of the upper papillate zone; nor are they to be found in or above this zone, nor at any point on either surface of the tentacular fold. The multicellular glands may be identified on surface preparations, but an insight into the histological relations is first afforded by sections. With hæmatoxylin the cell body stains lightly but uniformly, the mass at the distal end more deeply (Fig. 12), but with this stain no nuclei can be found either in the cells or in the connective-tissue investment of the gland. Each gland is seen to be made up of a number of flask-shaped cells, which are separated by thin partitions and which unite at their distal ends into a duct piercing the cuticula and opening upon its surface to the exterior. Andreae ('81, p. 216) was unable to find any nuclei in these cells. The application of a carmine stain, however, shows their presence near the proximal ends of the cells (Fig. 14), where they often lie flattened against the cell membrane by the crowding of the granules accumulated in the cell plasma. The same stain demonstrates also (Fig. 13) smaller nuclei at various points in the connective-tissue investment. There is likewise seen to be a difference in the cells of any one gland which indicates alternation in secretive activity. Thus the plasma of some cells is thickly crowded with large granules, which are entirely wanting in other cells. This is most clearly demonstrated in a transverse section of the gland, as shown in Figure 13. The cells differ in intensity of color to correspond with the number of granules present, and large distended cells are found near those which are evidently thinner and poorer. The product of these glands is a substance more waxy than fluid, to judge from its manner of caking in the duct, and breaking up into small fragments, like sebaceous material. Its discharge is evidently gradual like its production; for I have never found a gland empty, nor does the total amount of secretion present vary greatly. This alternation in functional activity between the various cells of one gland and the constancy

[1] For this suggestion, and the observation that such a tube exists, at least for S. Gouldii, I am indebted to my friend, Mr. C. B Davenport.

of secretion from the gland as a whole stand in strong contrast with the resting and active stages in secretion as found in the bicellular glands. The function of the secretion from the multicellular glands is probably more general, since the glands are so uniformly distributed over the surface of the body.[1]

One of the most peculiar points in connection with these glands is their relation to the nervous system. In almost every instance, a nerve fibre can be clearly traced from the subdermal plexus to the proximal end of the gland, and on fortunate sections (*gl.''' n. fbr.*, Fig. 14) it was possible in a number of cases to demonstrate an actual connection between gland cell and fibre, in that the former was prolonged into a delicate fibril, which, passing out from the glandular cavity in company with similar fibrils from the adjacent gland cells, entered within the neuroglia into the substance of the nerve and appeared to make up its fibrillar structure. This connection of gland cell with nerve fibre is found in all regions of the body, and is not confined, as Andreae maintained, to the posterior tip (Eichel) of the animal. In spite of this direct nervous connection, there seems to be little ground for regarding these structures as sensory organs, the interpretation put upon them by Leydig ('61) and others after him. A careful examination brought to light only the single kind of cells, which are in no way comparable with sensory cells. On the other hand, it may be said that a rich nervous supply is not without parallel for glandular structures.

The capsules of these glands are very thick, and nuclei are found on the partitions between the cells, showing that each cell is enclosed in a separate investment. But the partitions are never as strong as the general sheath of the entire gland, which possesses nearly the optical appearance of muscular elements. The variations in size are so great, being from $40 \times 50\,\mu$ to $90 \times 150\,\mu$ in the same region of the body, that the probability of a muscular capsule suggests itself strongly.

Allusion has already been made to the relation of the glands to the papillæ. In each papilla of the posterior zone, one finds at its tip an indefinite crowded mass of multicellular glands, and in an irregular double or triple row across the basal half, the bicellular variety. All of these open upon the external convex surface of the papilla. That the relation of glands to papilla is an intimate one, first appears clearly from the formation of the latter. As it is evident that new papillæ must be added with the growth of the animal, it is of interest to note the steps in the formation of these structures. The first indication is an evident

[1] See Addendum.

crowding of the otherwise scattered multicellular glands in the centre of some interspace of more than average size. Then the bicellular glands make their appearance as a loose double row, and so quickly that no intermediate stage could be found. They grow more crowded, and soon after their appearance a shallow furrow may be seen to enclose the mammiform area which they occupy. The skin seems to be tucked in on the three sides at once, and as the furrow grows deeper the papilla becomes more and more prominent. The growth in any papilla is increase in breadth rather than in length, so that the relative dimensions gradually change, and the older papillæ in any region are markedly wider than those more recently formed, while the length remains nearly constant throughout the entire zone.

Sense Papillæ. — The papillæ of the anterior zone are thickenings or modifications of the hypodermis, rather than typical papillæ like the posterior ones; they correspond probably to the "Wimperdrüsen" of Vogt und Yung ('88, p. 406). They are externally marked as small rounded prominences of the skin, varying in diameter from .15 to .40 mm., and often exhibit an oval or dumbbell-shaped opening in the centre of the prominence. Viewed in cross section (Plate II. Fig. 18) they display an evenly rounded contour, which is surmounted by cilia. These are short on the lateral margins of the area, but increase in length as they approach the apex, where they are longest. If one notices the basement membrane, here for the first time well developed, it will be seen that the prominence is almost entirely due to the increased height of the hypodermal cells, which have changed their form from that of the usual hypodermal elements so as to assume the character of filamentous cells, such as compose the hypoderm of the tentacles, with which they are identical. The isolated elements of the latter (Plate II. Fig. 21) might, indeed, answer equally well as types of these cells. In addition to the elongated nuclei of these cells, some few rounded ones are seen scattered between the filamentous cells, more usually near the basement membrane. Perhaps more common than the normal expanded form of the papillæ, just described, is the retracted condition shown in Figure 17. Such are found in all degrees of contraction, alternating irregularly with the normal form. The papilla figured is perhaps fully retracted, and one notes that the apical area lies sunk in the structure, so as to give the effect of a cavity and a duct. That this is due in part to the contraction of the cells themselves, and in part to the retraction of the central portion of the papilla, is clear from a comparison of Figures 17 and 18. In spite of this, I was unable to identify any muscular elements connected with the organ, the many

fibres which are attached to the proximal side of the basement membrane being, in refractive power and other optical properties, and in the character of their nuclei, indistinguishable from the other cutis fibres. One often finds such an appearance as is given in Figure 16. This is evidently a tangential section of a similar organ; the central clear space represents the hollow produced by the retracted apical area, and the apparently round nuclei are merely the elongated forms transsected. The appearance of the cells suggests no glandular nature, and nothing could be found resembling a secretion. For this reason I am inclined to question the propriety of the name "Wimperdrüsen" (Vogt und Yung, '88, p. 406), and to regard them as simple sensory organs. The retraction of the apical area would then be a simple method for protecting the long and delicate cilia during the advance of the animal through sand, similar to that reported by other observers for such organs in various groups. I was unable to discover any nerves connected with these organs, so that their sensory nature remains unproved, although none the less probable (Eisig, '87, p. 548). The structures just described are distributed over the aboral surface of the tentacles in somewhat irregular lines, becoming less frequent toward the margin of the fold, but are not present on its oral aspect. They suggest strongly the diffuse sensory organs (Becherorgane) of Capitellidæ, described by Eisig ('87, p. 547), but they are certainly less highly differentiated in the following respects: — 1. The cilia are not confined to the apical area (Polfeld), but are more or less diffused over the entire prominence. 2. There are only a few of the nervous nuclei (Körner) present in the basal portion. These structures recall the cup-shaped organs of Capitellidæ most strongly in the character of their elements, the filamentous cells, in their relation to the general hypodermis, and in the thin cuticula which covers them. In both cases, connection with nervous elements remains a matter of conjecture.

Very similar organs have been described by Spengel ('80, p. 465) for Echiurus, as appears at once from a comparison of the figures given by that author (Taf. XXIV. Figs. 21, 22). These, however, differ materially from those in Sipunculus in two respects: first, no cilia were present (Spengel believes them to have been lost through poor preservation); secondly, a fact of more importance, a large number of unicellular glands are found immediately below and in connection with these organs in Echiurus. The latter are certainly not present in Sipunculus. The distribution of these organs is quite different in the two forms, since there occur from one to seven on each of the papillæ of Echiurus, whereas in Sipunculus they are confined to the small anterior zone of the introvert.

e. Muscular Layers.

Of the muscular layers the diagonal is not present in the introvert. The circular layer, which is banded throughout the rest of the body, fuses at the end of the integumentary areas into one continuous sheet, and grows gradually less important anteriad, being almost entirely wanting in the anterior zones. The longitudinal muscular bands do not fuse until the middle of the posterior papillate zone is reached. From this point anteriad they also become reduced so that in the smooth zone the entire muscular layer measures but 70 to 90 μ in thickness. This remnant passes over into the retractors in a manner to be described in treating of the tentacular musculature.

2. Tentacular Fold.

A cross section of the tentacular fold shows that it consists of two layers of skin, which form the oral and aboral walls of an irregular cavity, traversed perpendicularly by numerous trabeculæ binding the two sides together (Fig. 3). This cavity is the extension of the so-called blood system, and is often found more or less filled with a coagulum. The character of the oral and aboral walls of this cavity differs: the structure of the oral portion will be considered first.

a. Oral Wall.

The cuticula (Plate III. Fig. 23) is extremely thin, never exceeding 2 μ, and usually appearing as a fine double contour. It is pierced by many pores for the exit of the fine cilia, which cover this surface from the apex of the fold down into the mouth. Evidently the inversion of surfaces in the retracted condition of the introvert led Selenka ('83, p. xvii) and others to regard the oral surface of the tentacles as without cilia, and to maintain that the aboral surface was ciliated, exactly the reverse of which is true.

The hypodermis (Plate III. Fig. 23) is composed of very high cells, which are in contact merely by their distal ends. Proximally they are prolonged into delicate processes, by which they are attached to the basement membrane. These cells are of the type of filamentous cells (Hautfadenzellen) described by Eisig ('87, p. 300). Lying nearly in the centre of the cell is the elliptical granular nucleus, which measures 11 by 4 μ. These cells are exactly similar to those contained in the sensory organs before described. Some such cells are seen in Figure 21, *d*, *f* (Plate II.). In addition to these there are occasional cells in the hypoderm, the nuclei

of which are narrower and stain much deeper, which possess a denser, more highly refractive cell body. Figure 21, *a*, *c*, *e*, represents these cells, which are seen *in situ* at *cl. sns.*, Figure 23. These may be sensory cells; I was, however, unable to discover the sensory hairs described by Selenka ('83, p. xvii) as found on the external surface; these cells certainly possessed merely such cilia as those adjacent. At the level of the mouth there is a transition from these filamentous cells to the columnar cells of the intestinal tract. This serves to fix the level of the oral opening proper, which would otherwise be indefinite on account of the various degrees of expansion or contraction of the animal.

b. Migratory Corpuscles.

Between these filamentous cells are found at varying heights highly refractive spherical nuclei 4 μ in diameter. My attention was first called to them in a preparation stained by Hamann's carmine (Plate II. Fig. 15), where they become prominent by reason of their being stained deeper than the other nuclei. A more careful examination showed that they were not accidental, as at first surmised, but definite independent structures. Each is surrounded by an irregular clear zone varying in width from a mere line to one half the diameter of the nucleus. By means of these peculiarities, such cells were traced back through the cutis, where they were most abundant in the spaces just below the basement membrane, to the blood cavity, and were found to agree precisely in size and optical character with one kind of blood corpuscle found in the coagulum there. They may then be regarded as migratory corpuscles or leucocytes, analogous perhaps to those of vertebrates. Similar cells are often met with, though never in such numbers, throughout the body wall.

The thin basement membrane to which the processes of the filamentous cells are attached is not everywhere equally distinct. Owing to the contraction of the different areas, it may be thrown into extensive and complicated folds, which, combined with the basal processes of the filamentous cells, render its identification a matter of difficulty, but in suitable regions it may be identified beyond a doubt.

Beneath this membrane lies a cutis, very similar to that of the body wall. It differs chiefly in the scarcity of pigment cells and in the entire absence of glands. The "Wimperdrüsen" seen by Vogt und Yung ('88, p. 406) on the oral surface of the tentacles, are merely appearances due to unequal contraction of certain areas, which produces structures superficially similar to the sensory organs of the anterior papillate zone already described. The cutis is further peculiar in the possession of

numerous muscular elements, which are primarily arranged about the blood cavity. The relation of these to the body musculature is of considerable interest.

c. Musculature.

If a transverse section be made in the plane of the annular mass of muscle surrounding the pharynx which is produced by the fusion of the four retractors, there appears only an indefinite mass of confused fibres. If, however, the section be cut in any longitudinal plane, it will be seen that the longitudinal fibres which compose this mass divide into two unequal parts, each of which draws its fibres from all parts of the original muscular mass. In such sections each of these portions appears like a band; the smaller curves over into the muscularis of the body wall of the introvert, or rather goes to form the longitudinal muscles of this, its fibres being directly continuous with those of the predominant longitudinal layer. The other and larger portion ascends into the tentacular fold; a few of its fibres follow the aboral surface of the blood cavity, but by far the greater number are continuous as an apparent muscular band along the oral side of the cavity immediately adjacent to the latter. At the base of the tentacular fold it is thickest, measuring half the thickness of the oral wall in which it lies; but as it advances distad through the tentacular fold, fibres are continually given off peripherally, so that they radiate toward the surface. These terminate in the vacuolated portion of the cutis in some manner not exactly determined. In this way the muscular band becomes looser and looser by the gradual loss of its elements, until at the tip of the tentacle only a few fibres remain, which attach themselves there. In cross sections the tentacular fold shows a few circular fibres, immediately adjacent to the blood cavity, which turn into the trabeculæ and cross into the corresponding layer of the opposite wall of the fold. In addition to these, the trabeculæ have other fibres which cut the muscular band at right angles, and run from one side of the tentacular fold to the other. At the outside of the muscular band there can be found usually a few circular fibres. If one considers that this muscular band, prominent in longitudinal sections through any plane, thus represents a muscular sheet extending throughout the whole tentacular fold, and that this lies in the cutis of the oral, or in an expanded condition *convex*, surface of the blood cavity, with its fibres radiating into every fold of the tentacles, — if one remembers, further, that it is at its base connected with the fused retractors, and is in fact merely an extension of them, — then its action in the inversion of the tentacles by drawing in and packing together

the various folds and plaits becomes at once clear. Furthermore, the muscles concerned in emptying the blood cavity are primarily the powerful trabeculæ and the longitudinal muscles, whereas the circular muscles, which are comparatively scanty, are only of secondary importance.

The cutis of the oral fold contains also numerous vacuoles in groups near the basement membrane, and these may be seen in transverse sections filled with the migratory cells previously mentioned. In addition to these small leucocytes, occasional larger granular cells are found in the lacunæ. These correspond again to the granular corpuscles of the blood. They do not make their way into the hypodermis. A tissue which might be homologized with the supporting tissue of Phoronis does not, according to my observations, exist in this form.[1]

Lastly, lining the blood cavity and covering the trabeculæ is an endothelium of very flat cells with proportionally large nuclei. This endothelial lining is continuous, and is adjacent to a mass of gelatinous connective tissue, which is without vacuoles, so that the blood corpuscles could reach the hypodermis only by a definite migration through the endothelium and the connective tissue. The cavity is often distended by a coagulum which contains corpuscles that, as various writers have maintained, actually differ in size from those of the cœlomic fluid, so that a connection between the two cavities was regarded as improbable. I can confirm the statement of previous writers that no such connection exists. Yet as the corpuscles are in size between the extremes of those in the cœlomic fluid, and not far from the average (*cf.* the exact measurements of Brandt, '70, p. 3), it is not improbable, in view of the migratory tendency of the corpuscles already described, that the cœlomic fluid receives its quantum from the blood system by the active emigration of the corpuscles which are formed in that system. This was conjectured by Brandt ('70, p. 24), who had found, however, no evidence of such a tendency on the part of the corpuscles. The detailed and careful account of the vascular system given by him has been overlooked by many later investigators.

d. Vascular System.

In contradistinction to Sipunculus Gouldii and to Phascolosoma, the blood cavities of S. nudus are not in the form of regular vessels, but are indefinite lacunar spaces, traversed by trabeculæ at irregular intervals and extending throughout the whole tentacular fold, everywhere almost equally distant from the exterior.

[1] See Addendum.

Numerous facts have been adduced by Andrews ('90, p. 419) to prove the branchial nature of the tentacles in S. Gouldii, chiefly the circulation and the red coloring matter of the corpuscles. Certain structural and other peculiarities compel me to deny the respiratory nature of this system in S. nudus. As was pointed out by Brandt ('70, p. 23), the extreme thickness of the layer of connective tissue in the tentacles would militate against the opinion that respiration takes place to any considerable extent in this part. Furthermore, although I have watched S. nudus in aquaria for considerable periods of time, not only when they were lying upon glass, but also when they were on the surface of the sand, and in their burrows wherever these were adjacent to the glass so as to permit observation, I have seen the tentacles extruded but seldom, and never for more than a second or two, until the water had become so impure as to partially narcotize the animals. The respiratory value of the tentacles when retracted cannot be regarded as very important!

But the greatest objection to assigning a respiratory character to this system would seem to be the utter inadequacy of the internal mediation between the vessels and the cœlomic fluid. The possible importance of this system in a respiratory direction must be seriously questioned when one considers that the ring canal and the two blind sacs (in S. Gouldii but one!) buried in the connective tissue of the œsophagus, which at best expose but one half their surface to the cœlomic liquid, are the only means of transmitting oxygen from the so-called vascular system to the general body fluid. The observations of Keferstein ('62, p. 47) upon living animals — these were made on Phascolosoma elongatum of a few millimeters in length and fully transparent — showed a constant movement of the fluid, but no passage of it from the vessels into the tentacles, or *vice versa*, except under considerable pressure or violent injuries.

The probable lack of respiratory function in the vascular system cannot be extended to all Sipunculids. In this connection it is of great interest to notice that various species are provided (Selenka, '83, p. xix) with several or many branched lateral appendages attached to the blind sac. Such organs are found in Phascolosoma Semperi, P. maniceps, Phymosoma asser, Dendrostoma signifer, *et al.* All of these forms possess, according to the same author, long thin filamentous tentacles (*cf.* his generic descriptions and figures). This peculiarity suggests at once the probability of a respiratory nature for the tentacles; and its occurrence in single species of various genera would indicate that it is a secondarily acquired function.[1]

[1] See Addendum.

The numerous dermal canals close under the hypodermis of S. nudus are unquestionably of great value in respiration, and the region of the introvert, which is distinguished by thin cuticular and muscular layers, actually not so thick as the walls of the tentacular fold, presents a far greater surface for the transmission of oxygen directly to the cœlomic fluid than the entire vascular system.

Primarily, then, this system is hydrostatic, and this is probably its chief function in S. nudus. The dorsal and ventral vessels are reservoirs into which the fluid is driven by the contraction of the tentacular fold. On the other hand, the muscular walls of these vessels serve to force the fluid out into the lacunæ of the tentacular fold, and thus to move and expand the latter. The varying contraction of these two sets of muscular elements gives rise to the constantly changing form of the tentacles, as the fluid is driven to and fro. This movement might easily simulate, or even under certain conditions become, a circulation. Moreover, any method of killing which worked violent contraction would distort the tentacular fold by driving the fluid into the extreme distal ends of the lacunæ, or by drawing together the entire mass of the tentacular fold, and forcing the fluid back into the dorsal or ventral vessel. It is probably in this way that the lobed or cut form was produced, which has been given as the typical one in all generic descriptions hitherto published. It is worthy of notice that those animals which were killed with expanded tentacles showed the walls of both dorsal and ventral vessels almost in contact, whereas in those which had retracted their tentacles these vessels were so filled by masses of coagulum as to reach a considerable diameter. The probable function, then, of the dorsal and ventral vessels is to receive and hold the fluid forced out of the tentacles at the time of inversion of the introvert.

e. Aboral Wall.

The aboral wall of the tentacular fold differs from the oral chiefly in the undifferentiated condition of the hypoderm. The latter is here composed of low non-ciliated cells, identical with the hypodermis of the general body wall, except where it is elevated into the papillæ or sensory organs already described. Sensory cells are wanting. The cutis of the aboral wall lacks the vacuoles which characterize that of the oral wall, and there are only very few leucocytes to be found.

The thin cuticula, cilia, and sensory cells of the oral, as well as the general sense organs of the aboral, wall of the tentacular fold, show it to be a most important organ of touch. This view is strengthened by the

large nervous supply it receives from the brain direct. The cilia undoubtedly aid in propulsion of food particles into the mouth.

3. Nervous System.

a. Brain.

The supraœsophageal ganglion (*gn. su'œ.*, Fig. 3) lies dorsal to the blood sinus, between the two dorsal retractors, and is enveloped by an investment of connective tissue. The posterior surface (Plate II. Fig. 22) is marked by a considerable incision in the median plane, and the anterior dorsal margin bears numerous digitate processes, which project into the cœlomic liquid. In sagittal sections the brain appears nearly flat on its ventral side, whereas the dorsal aspect is considerably curved. As seen from transverse sections, however, the dorsal surface is plane, while a deep median furrow (Plate III. Fig. 25) penetrates the ventral wall. Posteriorly (Fig. 25) this is continuous with a partition which divides the brain into two symmetrical lobes. Anteriorly (Fig. 24) the partition fails, and the division is only indicated by the furrow. On the antero-ventral surface is the termination of the cerebral canal (*cf. infra*).

The entire ganglion is covered by a capsule (Fig. 25, *cps. enc.*), the origin of which can only be determined by the consideration of a series of transverse sections. Following such a series from a short distance posterior to the brain, it will be seen that the septum joining the two dorsal retractors is here fused with the dorsal wall of the œsophagus, in which lies the dorsal vessel. As the posterior extremity of the brain is reached, this septum rises upon the brain, covering its dorsal aspect, and still showing laterally the connection with the dorsal retractors. Immediately inferior to the brain lies the dorsal vessel (Fig. 25, *va. sng. d.*), or, anterior to this, the blood sinus, which is separated from the brain only by its own wall, which thus forms the ventral covering of the brain. The dorsal and ventral layers of the capsule are continuous on those parts of the lateral aspect of the brain where there are no outgoing nerve stems; but when the latter exist, a neighboring portion of the brain capsule is reflected over them to form the neurilemma (Fig. 25, *con't. tis.*). This composite capsule is made up of a loosely woven mass of fibres which often show a plaited arrangement. The discoid nuclei measure 3.5 by 5 μ, and are deeply stained in all coloring fluids. Inferior to this basketwork of fibres are found occasional nuclei, which stain very faintly and possess each a few small nucleoli. These are surrounded by a small amount of a granular substance, and are very similar to nuclei found in the midst

of the meshes of the brain itself. Passing inward from this external capsule and directly continuous with its elements, fibres penetrate the brain in every direction, either in definite strands, or in a delicate network surrounding the ganglionic cells (Fig. 25). The fibres which make up these meshes are finer than most of those composing the capsule itself, and recall strongly the finer elements of the cutis. With these they also agree in the possession of minute elongated nuclei, although the clear nuclei previously mentioned are by no means rare. These fibres surround each ganglionic cell with a definite covering (Plate III. Fig. 32) of interlacing elements from which others pass off tangentially to neighboring cells. (*Cf.* Rohde, '87, Taf. IV. Fig. 44–68.)

Ganglionic Cells. — None of the many previous writers on Sipunculus have considered the histological elements of the central nervous system more than cursorily, so that a more extended description of these may be of interest, especially for comparison with the recent exact determination of these elements in many other groups of worms. All the ganglionic cells which were so situated as to admit of a positive answer to the question of their polarity were unipolar, though by no means always unifilar. Such cells as were accurately determined were usually peripheral, since the mass of other fibres and the confusion of many cells make an accurate determination in the case of those cells which are located in the centre of the nervous mass often impossible. I am inclined to think that in the latter region there are multipolar cells, although the demonstration of these was not wholly satisfactory. The cells are uniformly without any proper cell membrane. Each lies enveloped in a covering of delicate connective-tissue fibres (Plate III. Fig. 32), which accompanies the fibrous processes in the form of a delicate sheath (neuroglia). These enveloping fibres are a part of the meshwork which has already been described as arising from its external capsule, and penetrating through the whole brain.

Of all the ganglionic cells, the smallest (Plate III. Figs. 24, 25, *cl. gn. I.*), which usually appear simply as nuclei measuring 6 by 4 μ (Fig. 30), are the most abundant. They are highly refractive, and show a great affinity for coloring matter. There is a nuclear membrane which is stained deeply, as are also the numerous (4 to 10) nucleoli; between the latter many minute chromatine granules are distinguishable with a high power. These nuclei seem somewhat irregular in shape, varying from circular to oval. This variation I regard as due to the direction of the plane of section, and consider the true form as oval. In most cases it is impossible to find even a trace of a cell body, and I was at first

inclined to doubt the presence of any recognizable cell substance, and consequently to compare them with the "Nervenkerne" described by Rohde ('87, p. 30). But at length fortunate staining and thin sectioning showed unmistakably the presence, in many cases at least, of an extremely small cell body, such as is shown together with the nerve fibre in Figure 31. It will be noticed that the nucleus is oval in this case, and that the nerve fibre proceeds from one of the small ends of the oval. This fact, as well as the variation in form noticed by careful focusing on the nuclei, would seem to warrant the assumption that these nuclei are uniformly oval. From the diminutive size and transparency of the cell body in comparison with the highly refractive nucleus, it is at once evident that the former can be seen only under the most favorable circumstances. Since I was unable to find any difference in position, size, or optical qualities between these and the other nuclei of similar size and appearance, I feel justified in maintaining the existence of such a cell body for all nuclei of the class.

The second sort of ganglionic cell (*cl. gn. II.*) is distinguished by the presence of a much larger cell body (Plate III. Fig. 29). The nuclei correspond so exactly to those of the first class that they can hardly be distinguished from them. I was unable to see that they were either more or less deeply stained, or that they were, on the average, larger or smaller than nuclei of the first sort. The great difference is in the cell bodies, which in this case are several times larger than the nucleus, measuring 20 by 14 μ, and always evident on account of their slight affinity for stains. One or more vacuoles of non-colored matter, the paramitome of recent writers, may always be found, and in favorable cases there can be seen such a distribution of these as is shown in Figure 32. The *paramitome* exists in the form of numerous peripheral vacuoles subjacent to the enveloping connective fibres, and possibly (?) surrounded by them. The nucleus lies in a zone of clear matter, while the *mitome*, or filar substance, appears densest external to this. Between these and the first sort of ganglionic elements there exists every possible transition, so that this class is but poorly marked off from the preceding one. The vast majority of these cells are, however, of approximately uniform size, and I therefore cannot agree with Nansen ('87, *note*, pp. 113, 114) when he maintains that such transitional forms forbid the grouping of these cells in different classes. Such intermediate forms serve rather to explain the development of the one type from the other, without detracting from the individuality of either class.

The third type is that of the large[1] cells, represented in Figure 28, Plate III. These vary considerably in size and shape; the mean longitudinal diameter is 55 μ, the transverse 40 μ. The cell protoplasm stains rather deeply, and is notably granular. These granules resolve themselves in the nerve processes into fine lines. Each large ganglionic cell contains a number of clear spaces, the paramitome, exactly similar to those already described for cells of the second class; and these are often arranged concentrically, and more or less regularly along the periphery of the cell. The single nucleus, 15 by 12 μ in diameter, is usually found nearer the end of the cell from which the nerve fibre emerges, and, in contrast with those already described, is stained only lightly. A nuclear membrane is very distinct, and there is one large nucleolus 2–3 μ in diameter. In rare cases two smaller nucleoli were found, never more. The nucleus also contains numerous fine granules of chromatine, which are very distinct in the matrix, which remains completely unstained. Nuclei of this class are not infrequently crescentic, with a clear space enclosed by the horns of the crescent, corresponding exactly to such forms as are figured by Rhode ('87, Taf. IV. Fig. 51 *et al.*). Although variable, these cells represent a more isolated type than either of the other classes, and intermediate forms, especially in nuclear appearance and structure, are rarely seen in the brain.

An examination of the ventral nerve cord in transverse section shows a preponderance of cells of the second class. The first class is poorly represented, though the size of the plasmatic portion varies greatly in different cells. Occasionally one finds cells which in their deep staining and nuclear appearance recall the large cells of the brain. But measurements showed one such cell to be only 24 by 30 μ and its nucleus 7 by 11 μ in diameter, dimensions which are far smaller than those of the average of the large cells in the brain. These cells do not seem to be regularly arranged in the ventral nerve cord, and no grouping could be found which suggested metamerism. The peripheral nervous plexi possess very few ganglionic elements, and these few are not reducible to the types present in the central nervous system, for they are invariably multipolar, and are situated at the crossing or branching of fibres.

[1] It is much better, for the sake of clearness in neurological terminology, to keep the term "giant cells" (Riesenzellen) for the huge elements in the nervous system of Nemertines, Annelids, *et al.*, as German writers have done, than, with Shipley ('90, p. 16) and Andrews ('90, p. 424), to apply the term to such cells as I have placed in the third class, to which the former are at most only remotely homologous.

The *internal structure of the brain* shows a strictly bilateral arrangement of the elements. A transverse section through the middle of the ganglionic mass is represented in Figure 24 (Plate III.). The fibrous matter is collected into two commissural masses, in which the fibres run both anteroposteriad, chiefly at the lateral extremities, and laterally, chiefly in the middle. The real relation of these commissures to each other is first seen in sagittal sections (Plate II. Figs. 19 and 20), where the fibrous matter has the form of a > with the apex directed forward. The dorsal arm of this > is prolonged backwards in two lateral horns, which are surrounded by ganglionic cells. The tips of these horns, cut transversely, are seen in Figure 25 (Plate III.). The similar ventral horns are the roots of the circumœsophageal connectives. From near the anterior apex of the > a small arm of fibrous matter is directed forward, as seen in a sagittal section of the brain near its left lateral margin (Plate II. Fig. 19). This becomes, in a median sagittal section, a small commissure cut transversely (*coms. a.*, Fig. 20), and separated from the brain by the connective-tissue capsule. This commissure is at its right side again connected with the brain, as already described, for the left extremity. Thus it resembles in its form and relation to the main fibrous mass of the brain the handle of a basket, the handle being directed forward. It lies, as can be easily seen from the figures, immediately below the surface of the cerebral organ, and its relation to that structure will be more fully explained later.

The arrangement of the ganglionic elements in the brain is somewhat definite. Ganglionic cells of the first sort are found in nearly every part, and make up all diffuse centres, where, however, transitional forms render their separation from the second class difficult. The former are most strongly marked at the tip of the dorsal horn (*cl. gn. I.*, Fig. 25), where they are very densely crowded. They cover also the lateral and dorso-lateral aspects of the dorsal commissure (Fig. 24) in similar dense masses. The anterior face of the fibrous matter is also almost exclusively occupied by cells of the first class; and from this region they extend a short distance ventrally. Here one finds a gradual transition into the ganglionic cells of the second class (*cl. gn. II.*, Plate II. Fig. 20, Plate III. Fig. 24), which occupy the entire ventral and posterior aspects of the fibrous matter. These cells also fill the space between the dorsal and ventral commissures, but are found dorsally only between the two lateral fibrous swellings on the lateral edges of the dorsal commissure. They are never so crowded as cells of the first class, and display no particular arrangement into clusters or groups.

The large ganglion cells of the third class (*cl. gn. III.*) are present in a somewhat limited number, and always in a definite position. They lie in the posterior third of the brain, on its medial posterior boundary (Figs. 19, 20,'25). The large fibres which pass off from these cells are easily seen to turn toward the opposite side of the body and to make their way into the ventral commissure, where they are lost to view, either because they are split up into a number of small ones, or from some other cause suffer a diminution in diameter. This crossing of fibres from cells on one side of the body to the connective[1] of the other certainly does not take place frequently in either of the other two groups of ganglionic cells. Wherever circumstances permitted the following of nervous processes in groups I. and II., these were seen to pass off towards the connective on the same side of the body as the cell itself.

b. Cerebral Nerves.

From either side of the brain two groups of nerves pass off; the anterior consists simply of the first tentacular nerve (*n. ta. 1*, Fig. 22, Plate II.); the posterior contains the second, third, and fourth tentacular nerves and the œsophageal connective. The tentacular nerves radiate from the brain to the aboral wall of the tentacular fold, and, splitting there into numerous branches, follow the aboral wall of the blood cavity toward the distal margin of the fold. The first tentacular nerve supplies that portion which was designated as the dorsal horn. Following the margin of the fold from this region toward the ventral line, its successive parts are seen to receive their nerve supply from the third, second, and fourth tentacular nerves successively. Each of these innervates about equal portions of the fold. I was unable to trace the ultimate termination of the nerves in this region.

The œsophageal connectives give off each three branches: (1) the splanchnic, (2) the muscular, and (3) the inferior muscular. The splanchnic is given off ventrally and medially immediately after the connective leaves the ganglion (*n. spl.*, Figs. 22, 25). It passes diagonally forward, — *not posteriad*,[2] *as stated by other writers*,[3] — and into

[1] I use the word *connective* in the sense first suggested by Lacaze-Duthiers, to distinguish the nerve fibres joining ganglionic nerve centres which are on the same side of the body, reserving the word *commissure* for such fibres as cross the median plane of the body.

[2] This nerve is turned backward in Figure 22, for the sake of clearness in the drawing. Normally, it extends forward *under* the ganglion.

[3] This relation is obscured when the introvert is slightly retracted, and even apparently reversed when the retraction is greater.

the circular muscles of the pharynx, where it terminates in a distinct ring at about the level of the middle of the brain.

At the point where the splanchnic nerve forms a ring around the pharynx one finds a few nerve cells, but they are few in number, and hardly deserve the name of a ganglion. From this ring it is easy to trace in serial sections the stems of the intestinal plexus, which are here large. This plexus lies in the connective tissue of the intestinal wall, and was first described by Andrews ('90, p. 405) for S. Gouldii. However, he failed to find a splanchnic ring, or any anterior connection of the plexus with the central nervous system.

The muscular branch (*n. mu. ret.*) passes off laterally from the middle of the œsophageal connective, and divides near the centre of the fused mass of the dorsal and ventral retractors into two branches, one of which traverses each retractor. Not far behind this branch there is upon the connective a small trunk (*, Fig. 22), which passes to the surface of the muscular mass, but which could not be traced farther. It remained doubtful whether this was a subsidiary muscular branch or of other value.

c. Ventral Nerve Cord and Plexi.

After the union of the two connectives, the ventral nerve cord thus formed floats a short distance free in the body cavity, and sends off numerous long nerves to the body wall. The first of these, the composite nerve of Andreae ('81, p. 248), is by no means always composed of eight branches in a single sheath, as stated by that author. The number varies from six to nine, and the size of the different trunks varies as well (Plate II. Fig. 22, *I.*). In fact, the later branches, which according to him consist of two trunks, one from each side of the nerve cord, not only show great variability in the size of these trunks (Fig. 22, *II.*), but also at times only a single trunk can be found, which then comes from but one side of the nerve cord. All these frequent irregularities point to a lack of metamerism in the nervous system. On reaching the body wall these nerves branch in a digitate manner through the muscles of the introvert, the main trunks being longitudinal, and do not form nervous rings around the body as in other parts of the wall. From these longitudinal stems large trunks pass outward through the musculature to the dermal plexus.

This dermal plexus lies in the cutis at its plane of union with the musculature, and consists of large longitudinal trunks (*plx. n. drm.*, Plate I. Fig. 4) with lateral anastomoses. From this network, fibres (*rm. gl.*)

pass outward through the cutis to the multicellular glands and to the hypodermal cells, as already described, as well as inward (*rm. mu.*) to the muscles. The existence of such a plexus has already been shown by Andrews ('90, p. 395) for S. Gouldii. To his description, which answers equally well for S. nudus, I can only add a few observations as to the histology of the nerve trunks. Each of these possesses a well defined sheath or neuroglia (*n'gl.*, Fig. 5), in which discoid nuclei (*n'gl. nl.*) measuring 2 by 4.5 by 6 μ are common. These nuclei lie either inside or outside of the membrane; they may be stained deeply, and contain many nucleoli. The substance inside the neuroglia has a distinct fibrillar appearance, and when these nerve stems were bent upon themselves so as to be cut transversely and still extend longitudinally within the same section, the fibrillæ appear in the transverse section as dots. These are also the fibres which are connected with the cells of the multicellular glands (*gl.''' n. fbr.*, Plate I. Fig. 14).

The existence of the peritoneal plexus found by Andrews ('90, p. 395) in S. Gouldii could not be demonstrated in preserved specimens. No doubt the examination of fresh material will show its presence in S. nudus as well.

4. Cerebral Organ.

This interesting structure may be considered under two heads: first, the canal; and secondly, the surface next to the brain, or the cerebral organ proper.

The canal opens, as already described, on the dorsal median line, just posterior to the tentacular fold (*can. o. ceb.*, Figs. 2 and 3). From this point it extends posteriad about 1.5 to 2 mm., to the anterior ventral surface of the brain, where it terminates blindly (*o. ceb.*, Fig. 3). From the marginal fold which surrounds the opening arise numerous longitudinal ridges, which traverse the entire canal, and give it in transverse section (*can. o. ceb.*, Plate III. Fig. 26) a branched appearance. In a surface view the walls of the canal appear thickly spotted with brown, and further examination shows this to be due to the presence of large numbers of the characteristic pigment cells, which are usually seen crowded in masses along the summits of the ridges (*cl. pig.*, Fig. 26). It is probably this canal which was found by Keferstein und Ehlers ('61, p. 47) in S. tesselatus. The canal is correctly figured (Taf. VII. Fig. 1, 2, *u*, *u'*), but they evidently mistook its true character, since they say: "Ausserdem sieht man vom Hirn zum Tentakelkranz *einen aus zwei Hälften bestehenden, dicken Strang* verlaufen, der dort endet, und an dem End-

punkte, wie man bei der Betrachtung von aussen her wahrnimmt, in der Haut von einer Gruppe kleiner Falten umgeben ist als wenn er *eine Röhre wäre* und hier nach aussen mündete."[1] Among recent writers, Vogt und Yung ('88, p. 404) mention and figure the "cerebral canal," without a more particular description of its structure or morphological relations.[2]

The histological study of the canal shows some features of interest. Its entire surface is lined by an extremely thin cuticula, which appears under high powers merely as a double contour, pierced by numerous short cilia. The cells of the ventral wall of the canal have the appearance of ordinary hypodermal cells, except that they bear cilia. The dorsal wall is made up of similar cells near the mouth of the canal, but these become higher as the brain is neared, until at the middle of the canal they have assumed the form of a high columnar epithelium with large nuclei. This condition is preserved up to the surface of the brain. When examined more closely, these cells are seen to be filled with granules of a highly refractive nature, especially at their distal ends, and may be regarded as the source of the more or less extensive coagulum always found at the basal end of the canal. We have here, then, the secretive portion of this organ.

In cross sections of the canal (Plate III. Fig. 26) one sees clearly a group of muscular fibres which is deflected from the circular layer of the body wall and encircles the canal in the form of a sphincter (*spht.*), which, although most marked at the opening of the canal, is present along its entire extent. The function is evidently to prohibit the entrance of extraneous matter during the forward motion of the animal, and to

[1] The Italics are not in the original.

[2] P. S. — Since writing the above, I have obtained access to a preliminary communication by Spengel ('77), and find that in this he has maintained "die Existenz eines vom Gehirn zur Basis der Tentakeln führenden, offenen Canales." Spengel was thus the first to arrive at the true form of this structure, but I cannot find that he has anywhere given a more detailed account of its morphological or physiological character. In the same paper he says: "Das Gehirn stellt sich als eine knopfartige Verdickung des diesen Canal auskleidenden, mit der Epidermis zusammenhängenden Epitheles dar." Against this interpretation it may be said that the embryological evidence of Hatschek ('83) makes it probable that the canal is secondarily formed. Furthermore, a histological examination of the parts shows that the brain is less closely connected with the cerebral organ than appears superficially, since the brain capsule separates the two completely, except at the entrance of the anterior commissure, which furnishes the nervous supply to the organ in question. A full discussion of these relations follows the histological description of the cerebral organ which is given later.

assist in changing the water contained in the canal. In the latter function it would be assisted by the cilia lining the canal.

At its posterior end the canal widens abruptly into a saucer-shaped cavity, which lies with its concave surface upon the antero-ventral face of the brain (Figs. 3, 20, 27), and includes a low rounded prominence (*o. ceb.*) which I regard as the cerebral organ proper. Macroscopically, this appears to be continuous with the brain, but internally the connective-tissue capsule separates it almost entirely from the ganglionic mass. The histological character of this prominence, and its relation to the brain, require more extended consideration.

When one examines a longitudinal section of this region (Plate III. Fig. 27), perhaps the most striking feature is the extremely prominent cuticula (4 μ in thickness), which covers exactly the convex surface, and only that portion, for at the margin of this convexity (†, Fig. 27) it passes abruptly over into the very thin cuticula of the canal wall. At each *lateral* edge of the cavity there is a considerable thickening of the cuticula, which extends a short distance into the subjacent tissue and has in cross section the outline of a small retort. The cuticula presents a sharp outer boundary, and there one finds no remnants of cilia in the sections, yet I am inclined to think that cilia are present in the living animal. For in preserved specimens the entire lower portion of this canal is filled with a granular coagulum, which might easily enclose and obliterate cilia, if indeed any were preserved in this deep and narrow canal, where fluids evidently could not readily penetrate. The lateral cilia, which are perfectly distinct in the anterior half of the canal, become gradually less so, until in the lower portion, which is filled with this coagulum, they entirely disappear. In partly macerated specimens this thick cuticula breaks up into small blocks along lines extending perpendicularly to the surface, so that one may reasonably assume that there is a ciliated condition of this surface in the living animal.

It is difficult to study the cells which underlie this cuticula, inasmuch as the cell boundaries are very indistinct; the most evident feature is the regular row of nuclei which lies close under the cuticula. From these a crowded mass of nuclei (*cl. gn.*?) and fibres extend at right angles to the surface into an irregular group of fibres (transsected in Fig. 27, *coms. a.*), — the anterior commissure already described. If one examines the nuclei, their resemblance in size, shape, and optical properties to those of the central nervous system is evident. An actual entrance of the fibres into this anterior commissure can also be easily observed. The connection of these fibres and nuclei with the hypodermal

cells is very difficult to prove in sections; but in a badly preserved and hence partially macerated preparation there was in many places a definite continuity of these cells with the fibres and underlying nuclei. The probability of a direct continuity of the hypodermal cells with the central nervous system through the anterior commissure seems to me to be strong evidence in favor of the special sensory nature of the organ. An examination of its morphological relations also yields much that is favorable to this view.

The existence of a glandular area, the direct connection of the organ with the central nervous system, and its median position near the anterior extremity of the body, all point to its close relationship to such sense organs as are cited by Dewoletzky ('87, p. 278), and as are common in the class Vermes. These have their origin, according to Dewoletzky, in "ein Paar flimmernder Hauteinstülpungen." Whether the same holds for this cerebral organ of Sipunculus can naturally be decided only upon embryological evidence. Hatschek ('83, p. 115) says that toward the close of the larval stage two "Wimpergruben" are formed, one on either side of and near the median line. Further, he says, "Es sind dies wohl Sinnesorgane die sich wahrscheinlich auch am erwachsenen Thiere werden nachweisen lassen." These would by their fusion produce an organ which, in position at least, would correspond to that which I have described; and from the absence of any other structure to which these Wimpergruben can be traced, it is allowable to assume their genetic connection with this cerebral organ until the development shall furnish positive evidence on the question. That this organ might be the apical area (Scheitelfeld) which, by the recession of the brain from the surface, had come to be connected with the exterior by means of a canal, is disproved by Hatschek's ('83, p. 108) observation that there is a complete separation of the ganglion from the body wall at the time of its retreat; according to the same author, the formation of the Wimpergruben was subsequent to this separation.

If, now, the other members of the group of Sipunculids be examined for similar structures, two cases are found which require consideration. Shipley ('90, p. 18) has described an infolding of the preoral lobe which extends to the surface of the brain, and from which a pair of retort-shaped tubes penetrate into the ganglionic mass, one at each dorsal lateral angle of the brain. The cells of the inner limb of the tubes secrete a black pigment. Andrews ('90, p. 418) finds in S. Gouldii two similar tubes proceeding from the lateral edges of a transverse pit anterior to the ridges of the ciliated cushion. These tubes extend into

the ganglionic mass, and contain a coagulum, but have no pigment. Comparing these two accounts with each other and with that just given of the cerebral organ in S. nudus, it will be seen that the tubes lack pigment in S. Gouldii, and that both tubes and pigment are wanting in S. nudus, unless the regions of thickening in the cuticula on the lateral aspect of the cerebral organ noted above be the rudiments of such structures. The optic nature claimed by Shipley for the tubes in Phymosoma agrees with their reduction or disappearance in the forms inhabiting the sand. The position of the organs would seem to indicate an homology between the ciliated cushion of S. Gouldii, the deep pit of the preoral lobe in Phymosoma, and the cerebral organ in S. nudus. As to the histological character of the organ in Phymosoma, nothing is found in the account of Shipley. Andrews describes that of S. Gouldii as ciliated and well supplied with nerves. The deep location of the organ in S. nudus may be merely for protection, or perhaps due to the development of the glandular area, or even necessitated by the recession of the brain from the surface. The canal is much longer in S. tessellatus, where the brain also lies deeper in the body, than in S. nudus. An analogous variation may be seen in the deep-seated lateral organs of the Enopla as compared with those of the Anopla.

Finally, if it be asked why the whole structure may not be regarded as a degenerate organ, of which the pigmented tubes were originally the active portion, I can only say that the active glandular area and ciliated canal cannot be explained on such an assumption, and still less can the special nervous supply. I studied the structure a long time with this idea in mind, but finally became convinced that it was untenable in every respect. Although the evidence is far from complete, I regard it as an actively functional organ, morphologically the equivalent of the ciliated cushion of Phascolosomes, and possibly with a more highly specialized function, since it certainly has a more highly differentiated form.

Such organs are by no means rare. Dewoletzky ('87, p. 277) has given a list of similar ones, and has considered at length their probable function, which he regards as "some sort of general perception as to the character of the surrounding medium."

IV. Conclusions.

If now the account I have given of certain points in the anatomy and histology of S. nudus be compared with that given by Andrews ('90) for S. Gouldii, it will be noticed that, while there is a general similarity, a

correspondence in details is wanting. The dermal glands are hardly more than similar in type, and a direct correspondence between the different kinds is not to be found; for the bicellular are entirely wanting in S. Gouldii, and the multicellular of S. nudus agree with neither group described for S. Gouldii. Whether the non-glandular organs of Andrews correspond to the small papillæ described above cannot be definitely determined, on account of the brevity of Andrews's description and the lack of figures. On the other hand, Andrews has emphasized the fact that a close agreement exists between the dermal bodies of S. Gouldii and those of various Phascolosomes. Again, in the arrangement of the musculature, in the uniform unbanded circular layer, in the absence of diagonal fibres, and in numerous other details, S. Gouldii is unlike S. nudus, and in the same degree that the former resembles Phascolosoma. In the light of these facts, a modification of the generic characters given by Selenka ('83) to Sipunculus, which include S. Gouldii in the same genus with S. nudus, would seem advisable.

Striking as is the similarity between the anatomy of the nervous system in the Annelids and in the Sipunculids, certain characteristic differences are worthy of note. The peripheral system of plexuses is very highly developed in the latter, and consists almost entirely of fibres, whereas the dermal plexus of Capitellids, Nemertines, and Polychæts is composed largely of ganglionic cells. In the ventral nerve cord of Sipunculids there is no metameric arrangement of the lateral branches, nor any concentrations of the ganglionic elements in the cord itself. On the other hand, there is present a splanchnic nerve and an intestinal plexus in both Sipunculids and Annulata, and the complicated structure of the supræsophageal ganglion in Sipunculus agrees in general with that of various Annelids and Nemertines.

As regards the histology of the central nervous system, it will be noticed that the description given in this paper for S. nudus corresponds closely with that given by Rohde ('87) for Chætopods, and by Bürger ('90) for Nemertines. It is of interest, however, to note more exactly the points of likeness and difference. If further investigation should lead to the discovery of a minimal cell body for the nervous nuclei (Nervenkerne) of Rohde, — and I think this probable on account of the extreme difficulty experienced by Bürger ('90, p. 106) and myself in finding this cell substance, — then these nervous nuclei would correspond in general character and occurrence with the first class of ganglionic cells described by Bürger in Nemertines, and with the first type in Sipunculus. The first class of Rohde agrees in general with the second of Bürger; but

both differ from the second type in Sipunculus in one important point, namely, their arrangement. While they are (always?) found grouped in clusters in the brains of Polychæts and Nemertines, such an arrangement is never unquestionably present in Sipunculus, though indications of a regular grouping were sometimes noticed. This may be regarded, perhaps, as indicating a less highly specialized condition in the Sipunculid nervous system. According to Rohde and Bürger, these cells have nuclei slightly smaller and more deeply stained than those of the first class. I did not find any such difference between the two groups in Sipunculus. The third type of cells in the Sipunculid brain shows also a general correspondence to Class III. of the Nemertines and Class II. of the Chætopods. In both Chætopods and Nemertines there exists a fourth type, — the paired "giant cells" of the central nervous system, with their accompanying "giant fibres." These are entirely lacking in the Sipunculids. No one of the large cells has acquired any uniform or considerable superiority of size over its fellows. Furthermore, no giant fibres can be found in the ventral nerve cord, so that these elements probably do not exist in the Sipunculid nervous system. This may be regarded as further proof of the lower grade of specialization in the Sipunculids.

The earlier investigators regarded these "giant cells" as "Bildungen ganz verschiedener Art" (Spengel, '81, p. 40), but the more recent writers incline toward the opinion that they are homologous throughout (Eisig, '87, and Friedländer, '89). Now, either these "giant cells" are neomorphic in both groups, and hence not at all homologous, or the Sipunculids were separated from the primitive stem before the separation of Nemertines and Annelids took place, and before the differentiation of these elements had been effected. A complete disappearance of giant cells and giant fibres in the Sipunculids is hardly probable, in the light of the persistence of these and all other nervous structures. This would put the origin of the Sipunculids farther back than has usually been maintained, and would make their relationship to the Annelids somewhat distant. Of importance in this connection is the simple undifferentiated condition of the ventral nerve cord, which shows no trace of a metameric concentration of ganglionic cells, such as is found in the Annelids. According to the researches of Andrews ('90), moreover, the lateral branches lack that metameric character which has heretofore been assigned to them, and I have been able to confirm this in part for S. nudus. Lack of metamerism in the adult, as well as in the larva, would serve to strengthen the view of only a remote relationship

between Annelids and Sipunculids, as has long been maintained by Hatschek ('80 and '83) on embryological grounds.

The existence of at least giant fibres has been proved for Echiurus by the researches of Greeff ('79) and Spengel ('80, p. 487), and more recently for Thalassema by Rietsch ('86, p. 402), so that the presence of corresponding ganglionic cells may be reasonably assumed. This is, then, a further ground for separating the Sipunculids from the Echiurids, and for assigning to the latter a closer relationship to the Annelids than the former have. This position has been defended from an embryological standpoint by Hatschek ('80, p. 71) and Conn ('86, p. 399).

In spite of the well known conservatism of the nervous system, I am well aware of the dangers of such conclusions based upon the study of a single system or a single form. The foregoing comparison is offered, then, merely as a new side light on the unsettled question of the position of the Sipunculids, and in the hope that the accumulation of evidence from various sources may some day bring a clear and full solution of the problem.

January 20, 1891.

Addendum.

During the correction of the proof-sheets there has appeared a second paper by Shipley ('91) on Phymosoma (P. Weldonii, *n. s.*). It is interesting to note that the gland cells there described (p. 114) correspond very closely to the multicellular glands of S. nudus, except that no connection with nerve fibres is reported. Shipley affirms positively (p. 115) "the absence of those skeletal cells which formed so interesting a feature" of P. varians (Shipley, '90, p. 9). That such a tissue does not exist in S. nudus has already been emphasized. This is then strong proof that it is an individual peculiarity of the one species, rather than an ancestral relic. In general the claimed relationship of Sipunculids and Phoronis seems to me to have little in its favor beyond the external similarity of the two forms.

It is a pleasure to see that Shipley and I have both arrived independently at the same conclusions regarding the vascular system. He ('91, p. 116) does not regard it as important in respiration, and explains the cæcal diverticula of the dorsal vessel, which might be looked upon as strengthening the view of its respiratory nature, as merely reservoirs for the increased overflow from the tentacles, which are exceptionally numerous in this species.

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EXPLANATION OF FIGURES.

All figures were drawn with the aid of an Abbé camera, unless otherwise stated. They represent without exception preparations of *Sipunculus nudus*, L. The method of staining and systems employed are indicated briefly for each specimen.

ABBREVIATIONS.

can. o. ceb. Canal of cerebral organ.
cl. gn. I., II., III. Ganglionic cell I., II., or III.
cl. fil. Filamentous hypoderm cell.
cl. pig. Pigment cell.
cl. sns. Sensory cell.
coms. a. Anterior commissure of brain.
coms. d. Dorsal " "
coms. œ. Œsophageal connective.
coms. v. Ventral commissure of brain.
con't. tis. Connective tissue.
cps. enc. Capsule of brain.
crnu. d. Dorsal horn of tentacular fold.
ct. Cutis.
cta. Cuticula.
gl.'' Bicellular gland.
gl.'' dt. Duct of bicellular gland.
gl.'' env. Envelope " "
gl.'' nl. Nucleus " "
gl.'' vl. Vacuole " "
gl.''' Multicellular gland.
gl.''' dt. Duct of multicellular gland.
gl.''' env. Envelope " "
gl.''' n. fbr. Nervous fibrilla to multicellular gland.
gl.''' nl. Nucleus of the multicellular gland.
gn. su'œ. Supraœsophageal ganglion.
h'drm. Hypodermis.
leu'cy. Leucocytes.
mb. ba. Basement membrane.
mit. Mitome.
mu. crc. Circular muscles.
n'gl. Neuroglia.
n'gl. nl. Neuroglia nucleus.
n. mu. ret. Nerve of retractors.
nl. sns. Nucleus of sensory cell.
n. spl. Splanchnic nerve.
n. ta. Tentacular nerve.
o. ceb. Cerebral organ.
or. Mouth.
pa'mit. Paramitome.
pap. Papilla.
pli. ta. Tentacular fold.
plx. n. drm. Dermal nerve plexus.
pr'c. dg. Digitate processes of brain.
rm. gl. Glandular branch of plexus.
rm mu. Muscular " "
spht. Sphincter of cerebral canal.
va. sng. d. Dorsal blood-vessel.
va. sng. v. Ventral blood-vessel.
z. lev. Smooth zone of introvert.
z. pap. a. Anterior papillate zone of introvert.
z. pap. p. Posterior papillate zone of introvert.

PLATE I.

Fig. 1. Anterior half of the introvert. The base of the figure corresponds to the middle of the posterior papillate zone. The slight contraction at the centre of the zona levis is not usually found. Camera outline. Simple microscope. × 3.

" 2. Anterior aspect of tentacular fold. The figure is diagrammatic only to the extent that secondary folds are omitted. Camera outline. Simple microscope. × 4.

" 3. Sagittal section of introvert. Diagrammatic in regard to details. Simple microscope. × 8.

" 4. Longitudinal section of body wall of introvert in the anterior portion of the posterior papillate zone. Muscles diagrammatic. Böhmer's hæmatoxylin. Zeiss 3. A. × 98.

" 5. Transverse section of body wall at about the region indicated by the line *gl.*" in Fig. 4. Hamann's carmine. Zeiss 1. D. × 370.

" 6–8. Sections of bicellular glands in the three dimensions of space. Kleinenberg's hæmatoxylin. Zeiss apochr. 4 mm. Oc. 6. × 425.

" 6. Soon after the beginning of secretion. The membrane dividing the two cells is shown at *.

" 7. At the period of greatest activity in secretion.

" 8. At the close of secretive activity.

" 9. Transverse section of duct of bicellular gland immediately below the cuticula. Zeiss apochr. 4 mm. Oc. 6. × 425.

" 10, 11. Longitudinal and transverse sections of bicellular glands to demonstrate position of nuclei. Hamann's carmine. Zeiss apochr. 4 mm. Oc. 6. × 425.

" 12–14. Multicellular glands. Zeiss apochr. 4 mm. Oc. 6. × 400.

" 12. Longitudinal section. The duct is filled with a secreted material. Kleinenberg's hæmatoxylin.

" 13. Transverse section. At the left centre of the section a cell has fallen out. Hamann's carmine.

" 14. Longitudinal section to demonstrate nuclei and connection of gland cells with nerve fibres. Mayer's cochineal.

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gn su ce
prc dq
va snq d
van oeb
or
va snq v
7.
hdrm
cta
gl vl
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plx ndrm
cl pig
cl pig
rm mu
rm gl
ngl nl
ngl
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gl vl
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PLATE II.

Fig. 15. Transverse section of epithelium of tentacular fold to show the leucocytes *in situ*. Hamann's carmine. Zeiss 1. E. × 500.

" 16–18. Sense papillæ from anterior papillate zone of introvert.

" 16. Tangential section through a single papilla. Hamann's carmine. Zeiss 1. D. × 300.

" 17. Transverse section. Apical area retracted. Hamann's carmine. Zeiss 1. D. × 330.

" 18. Transverse section. Papilla fully expanded. Orth's picro-litho-carmine. Zeiss 1. D. × 220.

" 19. Lateral sagittal section of brain at point of departure of the anterior commissure from the central fibrous mass. Plane of section indicated on Figure 22 by dotted line "19." Mayer's cochineal. Zeiss 1. A. × 50.

" 20. Median sagittal section of brain. Plane of section indicated on Figure 22. Mayer's cochineal. Zeiss 1. A. × 50.

" 21. Cells of tentacular epithelium isolated by maceration; *a*, *c*, and *e*, sensory, *b*, *d*, and *f*, filamentous cells. Zeiss apochr. 4 mm. Oc. 8. × 725.

" 22. Central nervous system. Composite figure from maceration preparations controlled by serial sections. The splanchnic nerve (*n. spl.*) should project *forward* under the brain. For the sake of clearness it is represented as if turned posteriad; * denotes inferior muscular branch (?). The numbers denote the planes of sections represented in Figures 19, 20, 24, and 25. × 8 (about).

22

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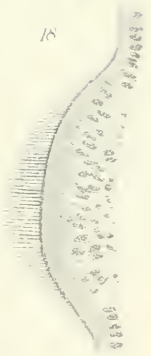
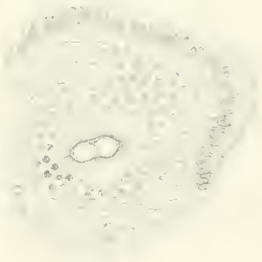


19



17

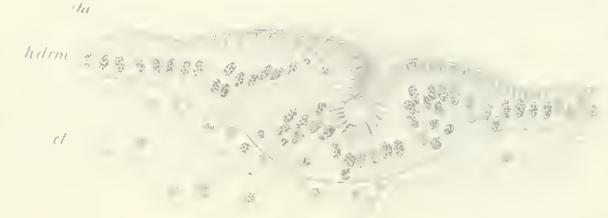


PLATE III.

Fig 23. Transverse section of hypodermis of tentacular fold with sensory cells. Weigert's picro-carmine. Zeiss apochr. 4 mm. Oc. 8. × 725.

" 24. Transverse section of brain. Plane of section shown in Figure 22, Plate II Grenacher's alcoholic borax carmine. Zeiss 1. A. × 50.

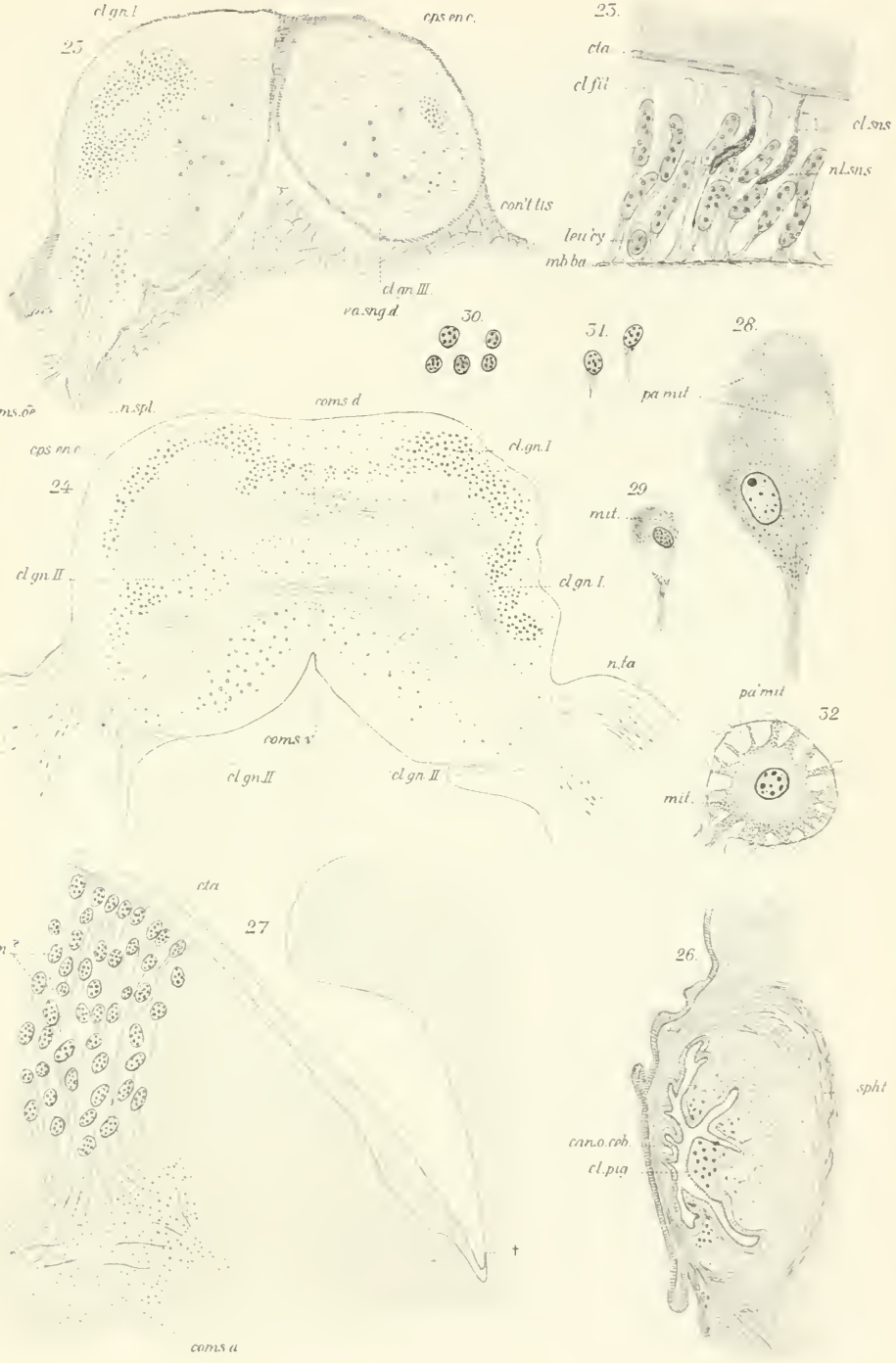
" 25. Transverse section of brain. Plane of section shown in Figure 22, Plate II. The section was cut somewhat obliquely, and the right half lies posteriad. Grenacher's alcoholic borax carmine. Zeiss 1. A × 50.

" 26. Transverse section of body wall passing through the canal of the cerebral organ at about the middle of its course. The left of the figure is dorsal. Hamann's carmine. Zeiss 1. A. × 50.

" 27. Transverse section of the cerebral organ: only one half is represented, and but a small section is drawn in detail. The cerebral canal begins at the angle near the number 27, and extends forward at right angles to the surface marked *cta*. The transition from the cuticula of the cerebral organ to that of the canal is marked by a †. Czokor's cochineal and picric acid. Zeiss apochr. 4 mm. Oc 8. × 510.

" 28–31. Ganglionic cells. Zeiss apochr. 4 mm. Oc 8. × 510. Fig. 28, Class III. Fig. 29, Class II. Fig. 30, Nuclei of Class I. Fig. 31, Class I.

" 32. Oblique section through a ganglionic cell of Class II., showing the regular arrangement of the paramitone. Hamann's carmine. Zeiss apochr. 4 mm. Oc. 8. × 725.


cl gn I
cps en c
25
con'l tis
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va sng d
23.
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No. 4. — *Three Letters from* Alexander Agassiz *to the* Hon. Marshall McDonald, *United States Commissioner of Fish and Fisheries, on the Dredging Operations off the West Coast of Central America to the Galapagos, to the West Coast of Mexico, and in the Gulf of California, in charge of* Alexander Agassiz, *carried on by the U. S. Fish Commission Steamer "Albatross,"* Lieut. Commander Z. L. Tanner, U. S. N., *Commanding.*

I.

Steamer Albatross, Panama, U. S. of Colombia,
March 14, 1891

My dear Colonel McDonald: —

We returned yesterday from our first trip. The route extended from Panama to Point Mala, and next to Cocos Island; from there we ran in a southerly direction, then northwesterly to Malpelo Island, and back to the hundred-fathom line off the Bay of Panama. We spent several days trawling off the continental plateau of the Bay. This trip being rather in the nature of a feeler, I cannot tell you just what I think it means. But I believe I can to some extent conjecture probabilities from what has been accomplished.

I have found, in the first place, a great many of my old West Indian friends. In nearly all the groups of marine forms among the Fishes, Crustacea, Worms, Mollusks, Echinoderms, and Polyps, we have found familiar West Indian types or east coast forms, and have also found quite a number of forms whose wide geographical distribution was already known, and is now extended to the Eastern Pacific. This was naturally to be expected from the fact that the district we are exploring is practically a new field, nothing having been done except what the "Albatross" herself has accomplished along the west coast of North and South America. The "Challenger," as you will remember, came from Japan to the Sandwich Islands, and from there south across to Juan Fernandez, leaving, as it were, a huge field of which we are attacking the middle wedge. As far as we have gone, it seems very

evident that, even in deep water, there is on this west coast of Central America a considerable fauna which finds its parallel in the West Indies, and recalls the precretaceous times when the Caribbean Sea was practically a bay of the Pacific. There are, indeed, a number of genera in the deep water, and to some extent also in the shallower depths, which show far greater affinity with the Pacific than with the Atlantic fauna. Of course, further exploration may show that some of these genera are simply genera of a wider geographical distribution; but I think a sufficiently large portion of the deep-sea fauna will still attest the former connection of the Pacific and the Atlantic.

I am thus far somewhat disappointed in the richness of the deep sea fauna in the Panamic district. It certainly does not compare with that of the West Indian or Eastern United States side. I have little doubt that this comparative poverty is due to the absence of a great oceanic current like the Gulf Stream, bringing with it on its surface a large amount of food which serves to supply the deep-sea fauna along its course. In the regions we have explored up to this time, currents from the north and from the south meet, and then are diverted to a westerly direction, forming a sort of current doldrums, turning west or east or south or north according to the direction of the prevailing wind. The amount of food which these currents carry is small compared with that drifting along the course of the Gulf Stream. I was also greatly surprised at the poverty of the surface fauna. Except on one occasion, when during a calm we passed through a large field of floating surface material, we usually encountered very little. It is composed mainly of Salpæ, Doliolum, Sagittas, and a few Siphonophores, — a striking contrast to the wealth of the surface fauna to be met with in a calm day in the Gulf of Mexico near the Tortugas, or in the main current of the Gulf Stream as it sweeps by the Florida Reef or the Cuban coast near Havana. We also found great difficulty in trawling, owing to the considerable irregularities of the bottom. When trawling from north to south, we seemed to cut across submarine ridges, and it was only while trawling from east to west that we generally maintained a fairly uniform depth. During the first cruise we made nearly fifty hauls of the trawl, and in addition several stations were occupied in trawling at intermediate depths. In my dredgings in the Gulf of Mexico, off the West Indies, and in the Caribbean, my attention had already been called to the immense amount of vegetable matter dredged up from a depth of over 1,500 fathoms, on the lee side of the West India Islands. But in none of the dredgings we made on the Atlantic side of the Isthmus did we come upon such masses

of decomposed vegetable matter as we found on this expedition. There was hardly a haul taken which did not supply a large quantity of water-logged wood, and more or less fresh twigs, leaves, seeds, and fruits, in all possible stages of decomposition. This was especially noteworthy in the line from the mainland to Cocos Island, and certainly offers a very practical object lesson regarding the manner in which that island must have received its vegetable products. It is only about 275 miles from the mainland, and its flora, so similar to that of the adjacent coast, tells its own story. Malpelo, on the contrary, which is an inaccessible rock with vertical sides, and destitute of any soil formed from the disintegration of the rocks, has remained comparatively barren, in spite of its closer proximity to the mainland.

The most interesting things we have found up to this time are representatives of the Ceratias group of Fishes, which the naturalists of the "Albatross" tell me they have not met before on the west coast of North America. The Crustacea have supplied us with a most remarkable type of the Willemoesia group. The paucity of Mollusks and also of Echini is most striking, although we brought up in one of the hauls numerous fragments of what must have been a gigantic species of Cystechinus, which I hope I may reconstruct. We were also fortunate enough to find a single specimen of Calamocrinus off Morro Puercos, in 700 fathoms, a part of the stem with the base, showing its mode of attachment to be similar to that of the fossil Apiocrinidæ. The number of Ophiurans was remarkably small as compared with the fauna of deep waters on the Atlantic side, where it often seems as if Ophiurans had been the first and only objects created. The absence of deep-sea corals is also quite striking. They play so important a part in the fauna of the deeper waters of the West Indies, that the contrast is most marked. Gorgoniæ and other Halcyonoids are likewise uncommon. We have found but few Siliceous Sponges, and all of well known types. Starfishes are abundant, and are as well represented in the variety of genera and species as on the Atlantic side of the Isthmus. I may also mention the large number of deep-sea Holothurians (Elasipoda) which we obtained, as well as a most remarkable deep-sea Actinian, closely allied to Cerianthus, but evidently belonging to a new family of that group. We found the usual types of deep-sea West Indian Annelids, occasionally sweeping over large tracts of mud tubes in the region of green mud. Although we dredged frequently in most characteristic Globigerina ooze, I was much struck with the absence of living Globigerinæ on the surface. Only on two occasions during a calm did we come across any number

of surface Globigerinæ and Orbulinæ. On one occasion the trawl came up literally filled with masses of a species of Rhabdamina closely allied to R. lineata. Thus far no pelagic Algæ have been met with.

It is interesting to note that at two localities we came across patches of modern greensand similar in formation to the patches discovered off the east coast of the United States by the earlier dredgings of the Coast Survey, of Pourtalès, and of the "Blake." Having always been more or less interested in pelagic faunæ, and having paid considerable attention to its vertical distribution during my earlier cruises in the "Blake," I was naturally anxious to reconcile the conflicting statements and experiences of the naturalists of the "Challenger" and "Gazelle" on one side, and my own observations on the other. Both Murray and Studer contended that, in addition to the deep sea and pelagic faunæ, there was what might be called an intermediate fauna with characteristic species, having nothing in common with the other two; while I maintained, on the other hand, from my experiments in the "Blake," that there was no such intermediate fauna, but that the pelagic fauna might descend to a considerable depth during the daytime to escape the effects of light, heat, and the disturbing influence of surface winds, and that this surface fauna on the Atlantic side — off shore in deep water — did not descend much deeper than 150 to 200 fathoms. In order to test this point, Dr. Chun, under the auspices of the Naples Station, made an expedition to the Ponza Islands. Dr. Chun applied to a tow-net an apparatus for closing it, similar to the propeller in use on our thermometer and water cups. He towed to a depth of 1,400 meters, if I am not mistaken, but never at any great distance from the mainland or from the islands of the Gulf of Naples, and came to the conclusion that the pelagic fauna existed all the way to the bottom. At the time, I considered his experiments inconclusive, and was of course anxious to repeat them in a strictly oceanic district, in great depths, and at a considerable distance from shore. I had an apparatus constructed by Ballauf of Washington, similar to that used by Dr. Chun. Unfortunately, in testing it we found the pressure of the tow-net against the propeller shaft so great as to make the machine useless, or at any rate, most unreliable. Thanks to the ingenuity of Captain Tanner, we overcame these obstacles. He devised a net which could be closed at any depth by a messenger, and which worked to perfection at 200, 400, 300, and 1,000 fathoms, and had the great advantage of bringing up anything it might find on its way up above the level at which it was towed. The lower part of the bag alone was closed by a double set of slings pulled

by two weights liberated from a bell crank by a messenger. We found that, in towing the net at 200 fathoms for twenty minutes, we got everything in any way characteristic of the surface fauna which we had fished up with the tow-net at the surface. In addition to this, we brought up five species of so called deep-sea Fishes, Scopelus, Gonostoma, Beryx, and two others, which had thus far been brought up in the trawl, and considered characteristic of deep water. Also a peculiar Amphipod, and the young of the new species of Willemoesia mentioned above. We then tried the same net at 300 and 400 fathoms, and in neither case did we bring up anything in the closed part of the bag, while the upper open part brought up just what we had found previously at a depth of 200 fathoms, plainly showing that in this district the surface fauna goes down to a depth of 200 fathoms, and no farther. Next came our single attempt to bring up what might be found, say within 100 fathoms of the bottom, and Captain Tanner's net was towed at a depth of 1,000 fathoms where the soundings recorded 1,100. Unfortunately, we deepened our water while towing only twenty minutes to over 1,400 fathoms, so that we failed in our exact object. But we brought up in the closed part of the bag two species of Crustacea, a Macruran and an Amphipod, both entirely unlike anything we had obtained before. I hope in the next cruise to follow this up, and determine also the upper limits of the free-swimming deep-sea fauna. In the upper part of the bag (the open part) we brought up a couple of so called deep-sea Medusæ, which must have been collected at a comparatively moderate depth, judging from their perfect state of preservation.

I can hardly express my satisfaction at having the opportunity to carry on this deep-sea work on the "Albatross." While of course I knew in a general way the great facilities the ship afforded, I did not fully realize the capacity of the equipment until I came to make use of it myself. I could not but contrast the luxurious and thoroughly convenient appointments of the "Albatross" with my previous experiences. The laboratory, with its ingenious arrangements and its excellent accommodations for work by day and by night, was to me a revelation. The assistance of Messrs. Townsend and Miller in the care of the specimens was most welcome, giving me ample time to examine the specimens during the process of assorting them, and to make such notes as I could between successive hauls, while paying some attention also to the work of the artist, Mr. Westergren. He has found his time fully occupied, and we have in this trip brought together a considerable number of colored drawings, giving an excellent general idea of the appearance

of the inhabitants of the deep waters as they first come up. These drawings can be used to great advantage with the specimens in making the final illustrations to accompany the reports of the specialists who may have charge of working up the different departments. . . .

We left Panama on the 22d of February, and returned to Panama after an absence of twenty days.

II.

ALBATROSS, ACAPULCO, April 14, 1891.

We have reached the end of our second line of explorations. After coaling we left Panama, and reached Galera Point, where we began our line across the Humboldt Current, which was to give us a fair idea of the fauna of that part of the coast as far as the southern face of the Galapagos. With the exception of three good casts, the trawling on that part of the sea bottom proved comparatively poor, nor did the sea face of the southern slope of the Galapagos give us anything like the rich fauna I had expected. Theoretically, it seemed certain that a sea face like that of the Galapagos, bathed as it is by a great current coming from the south and impinging upon its slope, and carrying upon its surface a mass of animal food, could not fail to constitute a most favorable set of conditions for the subsistence and development of a rich deep-sea fauna.

In the deeper parts of the channel between Galera Point and the southern face of Chatham Island we found a great number of Elasipoda, among them several genera like Peniagone, Bathodytes, and Euphrosine, represented by numerous species. The Starfishes of this our second cruise did not differ materially from those collected during our first trip, but we added some fine species of Freyella, Hymenaster, Astrogonium, Asterina, and Archasteridæ to our collections. Among the Sea-urchins on two occasions we brought up fine hauls of a species of Cystechinus with a hard test, many specimens of which were in admirable state of preservation. Among the Ophiurans nothing of importance was added, unless I may except a lot of Ophiocreas attached to a Primnoa, and a pretty species of Sigsbea attached to a species of Allopora, from the south side of Chatham Island.

The Gorgonians were remarkably few in number, which is undoubtedly due to the unfavorable nature of the bottom we worked upon. Nearly everywhere except on the face of the Galapagos slope we trawled upon a

bottom either muddy or composed of Globigerina ooze, more or less contaminated with terrestrial deposits, and frequently covered with a great amount of decayed vegetable matter. We scarcely made a single haul of the trawl which did not bring up a considerable amount of decayed vegetable matter, and frequently logs, branches, twigs, seeds, leaves, fruits, much as during our first cruise.

Our Crustaceans, from the nature of the bottom, naturally consisted of the same groups of deep-sea types which we obtained before. I may, however, mention a haul containing a goodly number of Nephrops, a genus we had not previously obtained.

Among the Worms the Maldaniæ and limicolous types were unusually abundant at some localities, the empty mud tubes often filling the bottom of the trawl. Some very large specimens of Trophonia were collected, and remarkably brilliantly colored (orange and carmine) Nemerteans and Planarians.

The Mollusks were very scanty, and the absence of Comatulæ or other Crinoids was equally disappointing, even when trawling on the extension of the line started three years ago by the "Albatross," on the eastern face of the Galapagos slope, when on her way from Chatham Island to San Francisco. We took up this line off Indefatigable Island, hoping to obtain from that quarter our best results, but our hauls were very disappointing. The ground proved not only most difficult to dredge upon, but also comparatively barren, and it was not till we got into the oceanic basin again, between the Galapagos and Acapulco, that our catches improved. But even then they were not to be compared with the hauls at similar depths in the Atlantic off the West Indies, or along the course of the Gulf Stream.

Among the Fishes, our most important catches were fine specimens of Bathyonus, of Bathybrissa, of Bathypteroides, and a few specimens of Ipnops in excellent condition.

From the nature of the bottom we naturally expected rich hauls of Siliceous Sponges, but we did not find many, and I do not think there are many novelties among those we have collected. On two occasions, a number of specimens of Ascidians were brought up; among them was a fine white translucent Corinascidia.

Among the Bryozoans, the most noteworthy haul was a number of beautiful specimens of the delicate Naresia, in excellent condition. On the line from the Galapagos to Acapulco we brought up a good many Foraminifera from the mud bottoms. On several occasions the bottom must have been covered with huge masses of a new type of an arena-

ceous Foraminifer, forming immense curling sheets attached by one edge to stones or sunk into the mud. This Foraminifer seems to increase in size by forming irregular more or less concentric crescent-shaped rings. When it comes to the surface, it is of a dark olive-green color.

During this second cruise we continued our experiments with the Tanner closing tow-net, in order to determine the lower limits of the surface pelagic fauna, and to determine also if there is any so called intermediate pelagic fauna at other depths, or within a short distance from the bottom.

On the 25th of March, at a point not quite half way between Cape San Francisco and the Galapagos, in 1,832 fathoms of water, the Tanner net was sent down to tow at a depth which varied from 1,739 to 1,773 fathoms. The net was towed within these limits for a period of something over twenty minutes. The messenger was then sent down to close the net; time occupied seven minutes. The net was then drawn up to the surface. The lower part of it was found to have closed perfectly, and contained nothing beyond a few fragments of leaves. The lower bag was carefully washed in water which had been strained, and the water examined with all possible care, and sifted again. It contained nothing. The upper part of the net, however, which had remained open on its way up, was found to contain the identical surface things which on former occasions we had found in the Tanner net down to a depth of 200 fathoms. They were a small species of Sagitta, and species of Doliolum, Appendicularia, a huge Sagitta, a large number of Leucifer and Sergestes, and several species of Schizopods and Copepods; two species of Hyperia, probably parasitic on a Salpa, which was also quite abundant; several finely colored Calanus, some Isopods, and a number of fragments of what must have been a very large Beroe, measuring from five to six inches in diameter; Leptocephalus, several specimens of Stomias, of Scopelus, of Melamphæs, and other species, many of which, like some of the Schizopods, had been considered as typical deep-sea forms. Among the so called deep-sea Medusæ, several specimens of Atolla and Periphylla were also found in the open part of the net. I may mention also as of special interest a huge Ostracod, allied to Crossophorus, with a thin semi-transparent carapace, and measuring somewhat more than one inch in length. The largest Ostracod previously known is not more than one third of an inch long. On two other occasions this same Ostracod was brought up in the tow-net from a depth of less than 200 fathoms.

The surface at this point was also examined with the tow-net, and the pelagic animals found to be the same as those brought up in the open part of the tow-net on its way from the bottom. The number both of species and specimens was, however, much less than in the Tanner net. On the following day the Tanner tow-net was sent to be towed at a depth of 214 fathoms. In twenty minutes the messenger was sent down and the net hauled up. The bottom part of the net came up tightly closed. Its contents were examined in the same manner as before in well sifted water, and the water was found to be absolutely barren, while the upper part of the net, which came up open, and was not more than eight or nine minutes on the way, was well filled with surface life. The net contained this time a number of Hyalæas and Criseis, in addition to the things collected the day before. An examination of the surface fauna at this same point with the tow-net showed the presence only in smaller numbers of the same species which the open part of the same net contained, except that there were a larger number of bells and fragments of Diphyes and of Cristalloides than in the Tanner net. The point at which this experiment was made was about 250 miles from the Galapagos, and about the same distance from Cape San Francisco. There were myriads of Nautilograpsus swarming on the surface of the water; they literally filled the surface tow-net. On two other occasions, once at a distance of 350 miles in a southeasterly direction from Acapulco (depth 2,232 fathoms), we tried the same experiment with the Tanner net, and invariably with the same result. The net was towed at a depth of 100, of 200, and of 300 fathoms, each time for twenty minutes, the messenger sent down, and the bottom part closed. At the depth of 100 fathoms, the closed part of the net contained practically the same things as the open part of the net; at 200 fathoms, the lower part of the net contained but few specimens of the surface life; and at 300 fathoms, the closed bottom net came up empty.

On the following day the surface was carefully examined, and the tow-net sent to 175 fathoms, where it was towed for twenty minutes, and the messenger sent down to close it. The lower net came up well filled with the surface pelagic species, which on this day were unusually varied, it having been smooth and calm the previous night, and the morning before the towing was made. This haul was made in the evening, at 8 P. M. The previous hauls had been made at about 10 A. M., in a brilliant sunlight. Again on the 11th of April, about thirty miles southeast of Acapulco, in a depth of over 1,800 fathoms, the Tanner net was sent to a depth of 300 fathoms, and the messenger sent down to close it.

There was nothing in the lower part of the net which had been closed, while the open part contained an unusually rich assortment of surface species, and among them a large number of Scopelus, of Schizopods, and of Rhizopods, mainly Collozoum and Acanthometra.

These experiments seem to prove conclusively that in the open sea, even when close to the land, the surface pelagic fauna does not descend beyond a depth of 200 fathoms, and that there is no intermediate pelagic fauna living between that depth and the bottom, and that even the free-swimming bottom species do not rise to any great distance, as we found no trace of anything within 60 fathoms from the bottom, where it had been fairly populated.

The experiments of Chun regarding the distribution of the pelagic fauna have all been made in the Mediterranean, within a comparatively short distance from the shore, and in a closed basin showing, as is well known, special physical conditions, its temperature to its greatest depths being considerably higher than the temperature of oceanic basins at the limit of 200 fathoms, or thereabout, which we assume now to be the limit of the bathymetrical range of the true oceanic pelagic fauna. At 200 fathoms our temperature was from 49° to 53°, while, as is well known, the temperature of the Mediterranean soon falls at 100 fathoms even to about 56°, a temperature which is continued to the bottom in this closed basin. Of course, if temperature is one of the factors affecting bathymetrical distribution, there is no reason except the absence of light which would prevent the surface pelagic fauna from finding conditions of temperature at the greatest depth similar to those which the surface fauna finds within the limit of 200 fathoms in an open oceanic basin.

Arriving as we did at the Galapagos at the beginning of a remarkably early rainy season, I could not help contrasting the green appearance of the slopes of the islands, covered as they were by a comparatively thick growth of bushes, shrubs, and trees, to the description given of them by Darwin, who represents them in the height of the dry season as the supreme expression of desolation and barrenness. Of course, here and there were extensive tracts on the sea-shore where there was nothing to be seen but blocks of volcanic ashes, with an occasional cactus standing in bold relief, or a series of mud volcanoes, or a huge black field of volcanic rocks, an ancient flow from some crater to the sea; but as a rule the larger islands presented wide areas of rich, fertile soil, suitable for cultivation. The experiments at Charles Island, where there is a deserted plantation, and at Chatham Island, where Mr. Cobos has under success-

ful cultivation a large plantation producing sugar, coffee, and all the tropical fruits, as well as extensive tracts on which his herds of cattle, sheep, and donkeys roam towards the higher central parts of the island, show the fertility of these islands. They are indeed as favorably situated for cultivation as the Sandwich Islands or Mauritius, and there is no reason why, if properly managed, they should not in the near future yield to their owners as large returns as do those islands.

I obtained from Mr. Cobos a piece of the so called sandstone said to occur on Indefatigable Island, and which of course I was most anxious to see, as the occurrence of true sandstone would have put quite a different face on the geological history of the Galapagos from the one usually received. This I found to be nothing but coral rock limestone, either a breccia or slightly oölitic, identical with the formation found back of the beach at Wreck Bay on Chatham Island. I found there an old coral rock beach, extending on the flat behind the present beach, composed entirely of fragments of corals, of mollusks, and other invertebrates, cemented together into a moderately compact oölitic limestone, which when discolored, as it often is and turned gray, would readily be mistaken for sandstone. This coral rock is covered by just such a thin, ringing coating of limestone as characterizes the modern reef rock of other localities. On nearly all the islands there are a number of sandy beaches made up of decomposed fragments of corals and other invertebrates, and cemented together at or beyond high-water mark into the modern reef rock I have described. The coral is mainly made up of fragments of Pocillopora, which is found covering more or less extensive patches off these coral sand beaches, but which, as is well known, never forms true coral reef in the Panamic district. The only true coral reef belonging to this district is that of Clipperton Island, (if we can trust the Admiralty charts,) situated about 700 miles to the southwest of Acapulco. But neither at Cocos Island, nor at the Galapagos, nor anywhere in the Panamic district, do we find true coral reefs, — nothing but isolated patches of reef-building coral. The absence of coral reefs in this district has of course already been noted by other naturalists, who have been struck by this feature in an equatorial region. Dana has ascribed it to the lower temperature of the water due to the action of the Humboldt Current coming from the south, pouring into the Bay of Panama, and then flowing westward with the colder northerly current coming down the west coast of Mexico and Central America. From the investigations made this year by the "Albatross," I am more inclined to assume that the true cause of the absence of coral reefs on the west coast of Central America is due

to the immense amount of silt which is brought down the hill and mountain sides every rainy season, and which simply covers the floor of the ocean to a very considerable distance from the land, the land deposits being found by us even on the line from the Galapagos to Acapulco at the most distant point from the shore to the side or extremities. The mud in Panama Bay to the hundred-fathom line is something extraordinary, and its influence on the growth of coral reefs is undoubtedly greatly increased from the large amount of decomposed vegetable matter which is mixed with the terrigenous deposits.

The course of the currents along the Mexican and the Central and South American coasts clearly indicates to us the sources from which the fauna and flora of the volcanic group of the Galapagos has derived its origin. The distance from the coast of Ecuador (Galera Point and Cape San Francisco) is in a direct line not much over 500 miles, and that from the Costa Rica coast but a little over 600 miles, and the bottom must be for its whole distance strewn thickly with vegetable matter. The force of the currents is very great, sometimes as much as 75 miles a day, so that seeds, fruits, masses of vegetation harboring small reptiles, or even large ones, as well as other terrestrial animals, need not be afloat long before they might safely be landed on the shores of the Galapagos. Its flora, as is well known, is eminently American, while its fauna at every point discloses its affinity to the Mexican, Central or South American, and even West Indian types, from which it has probably originated; the last indicating, as well as so many of the marine types collected during this expedition, the close connection that once existed between the Panamic region and the Caribbean and Gulf of Mexico.

I have already referred to the physiognomy of the deep-sea fauna, showing relationship on the one side to Atlantic and West Indian types, and on the other to the extension of the Pacific types, which mix with the strictly deep-sea Panamic ones. The western and eastern Pacific fauna, while as a whole presenting very marked features in common, yet also present striking differences. The vast extent of territory over which some of the marine types extend, through all the tropical part of the Pacific, may readily be explained from the course of the great western equatorial current and the eastern counter current, which cannot fail to act as general distributors in space for the extension of a vast number of marine Vertebrates and Invertebrates.

Mr. Townsend made quite a large collection of Birds from Chatham and Charles Islands, considering the short time we were there.

As soon as we have reached Guaymas, I shall be able to give you a better *résumé* of the character of the deep-sea fauna of the Panamic region, and of its relationship on the one side to the Pacific fauna and on the other to the West Indian region.

III.

GUAYMAS, April 25, 1891.

We left Acapulco on the 15th of April, for our third cruise, into the Gulf of California, and steamed as far as Cape Corrientes without attempting to do any trawling. The character of the bottom, as indicated on the charts, promised nothing different from what we had dredged off Acapulco, and on the line from there to the Galapagos Islands. We made one haul off Cape Corrientes, bringing up nothing but mud and decomposed vegetable matter. This induced us to keep up the Gulf of California, till we were off the Tres Marias. We there made several hauls, and obtained some Umbellulæ, Pennatulæ, Trochoptilum, Anthoptilum, and a fine Antipathes, a few Comatulæ, a large Astropecten, some fine specimens of Urechinus and of Schizaster, a few Holothurians, Lophothuria, Trochostoma, and two species of Elasipoda, besides a few fragments of Gasteropods, with an empty shell of Argonauta.

Among the Crustacea there came up the usual types found living upon muddy bottom, such as Glyphocrangon, Heterocarpus, Notostoma, Pentacheles, Nematocarcinus, Nephrops, together with species of Lithodes and of Munida. The usual types of limicolous Annelid also were found here, Halinæcia, Terebella, Maldania, and the like, a few Ophiurans, Ophiopholis and Ophiocantha, a few fragments of Farrea, and a huge Hyalonema of the type of H. toxeres. Among the Fishes there were a few Macrurans, Bathypteroides, Lycodes, and Malthe. The trawl was usually well filled with mud, and with the mud came up the usual supply of logs, branches, twigs, and decayed vegetable matter.

On going farther north into the Gulf of California, the nature of the bottom did not change materially, and we found the trawling most difficult from the weight of the mud brought up in the trawl. But occasionally a haul was made which more than repaid us for the time spent on the less productive ones. Two of the hauls are specially worthy of mention, as being characteristic of the deep-water fauna of the Gulf of California, one made in 995 fathoms, and the other in 1,588 fathoms. We obtained in these hauls a number of Ophiomusium and Ophiocreas,

some fine specimens of Schizaster, a new genus allied to Paleopneustes, and also the same species of Cystechinus, with a hard test, and of Phormosoma, which we had obtained before on the line from the Galapagos to Acapulco. Beside these, there came up a number of specimens of an interesting species of Pourtalesia, most closely allied to Pourtalesia miranda, the first type of the group dredged in the Florida Channel by Count Pourtalès.

The deeper haul was specially rich in Holothurians, among them a fine large white Cucumaria, some specimens of Trochostoma, several species of Bathodytes, some of them remarkable for their white color, their huge size, and comparatively small number of ventral tentacles. With these were numerous specimens of an interesting species of Euphronides. In this haul I was specially struck with the Elasipoda, and the great variety in the consistency of the skin in individuals of one and the same species; it varied in different individuals from extreme tenuity to a comparatively tough gelatine-like consistency. On carefully sifting the mud, we found a number of interesting Foraminifera, and of delicate and minute Gasteropods and Lamellibranchs, fragments of the shell of an Argonauta, and two species of a huge ribbed Dentalium. Among the Starfishes were specially noticeable a large Brisinga, a long-armed Cribrella, and several species of Astropecten. The usual types of Worms were found in the mud at these greater depths. In addition to a number of Macruroids, we obtained a pink Amphionus, a large black Beryx-like fish, a fine Nettastoma, and a couple of species of Lycodes. The usual surface species of Stomias and of Scopelus also came up in the trawl. Among the Crustaceans were a fine lot of Arcturus, of Colossendeis, of Glyphocrangon, and of a Caridid with a deep blue patch on the base of the carapace, making the strongest possible contrast to the dark crimson coloring of the rest of the body. Blue is a very unusual color in the deep-sea types, although the large eggs of some of the deep-sea Macrurans are often of a light blue tint.

We brought up in the trawl at various times, and subsequently also in the Tanner net, from depths of less than 200 fathoms, the same gigantic Ostracod which I mentioned in one of my previous letters, several specimens of Atolla, and fragments of a huge Periphylla, which must have been at least fifteen inches in diameter. Also a most interesting new type of Bougainvillia, remarkable for having eight clusters of marginal tentacles, but only four chymiferous tubes.

We continued our experiments with the Tanner tow-net. On the 16th of April, about 120 miles from Acapulco, we sent the net to tow

at a depth of 175 fathoms, and after towing for about twenty minutes sent the messenger to close it. On examining the bottom part of the net, which came up tightly closed, we found it to contain practically the same things as we obtained in the surface net at the same spot.

On two occasions we sent the net to be towed at depths of 800 fathoms and of 700 fathoms, the depths at these points being in one case 905 fathoms and in the other 773 fathoms. At the greater depth, the water shoaled somewhat while towing, as the closed part of the net came up partly filled with fine silt; while during the second haul, the twisting of the swivel wound the straps of the weights round the rope, and the net came up open, but must have dragged very close to the bottom, as it contained a fine specimen of Nettastoma, and some Penæids, which we supposed to be deep-sea types. Otherwise the net contained only the customary surface species of Sagitta, Pteropods, Copepods, Schizopods, Tunicates, and Fishes. These two hauls were made about the middle of the Gulf of California, at a distance of some fifty miles in a southwesterly direction from Guaymas.

On the 23d of April, a few hours before reaching Guaymas, we made one more attempt with the Tanner tow-net, at a depth of 620 fathoms, sending the net to be towed at a depth of from 500 to 570 fathoms. We found in this case in the bottom part of the net, which came up tightly closed, a Scopelus, a Penæid, and a Hyalea, while the upper open part of the net contained the same surface species we had obtained before.

My experience in the Gulf of California with the Tanner self-closing net would seem to indicate that in a comparatively closed sea, at a small distance from the land, there may be a mixture of the surface species with the deep-sea bottom species, a condition of things which certainly does not exist at sea in an oceanic basin at a great distance from shore, where the surface pelagic fauna only descends to a comparatively small depth, about 200 fathoms, the limits of the depth at which light and heat produce any considerable variation in the physical condition of the water. The marked diminution in the number of species below 200 fathoms agrees fairly with the results of the "National" Expedition.

The more I see of the "Albatross," the more I become convinced that her true field is that of exploration. She is a remarkably fine sea boat, and has ample accommodation for a staff of working specialists such as would be needed on a distant expedition. The time will soon come when the Fish Commission will hardly care to continue to run her,

and I can conceive of no better use for so fine a vessel than to explore a belt of 20° latitude north and south of the equator in the Pacific, from the west coast of Central America to the East Indian Archipelago.

The success of the "Albatross" thus far has depended entirely upon the zeal, energy, intelligence, forethought, and devotion of Captain Tanner, if I may judge of the past by the present. He never spares himself, and he is always ready to make the most of the time at his disposal for the benefit of the special object he has in charge. He looks after every haul of the trawl himself, and will not allow any one else to jeopard in any way the material of the vessel, or the time it requires to make a haul. That responsibility he assumes himself, and it constitutes his daily work. In looking over the records of the "Albatross" during her voyage from New York to San Francisco, I am struck with the amount of work which has been accomplished. It would be but a just return to Captain Tanner, if Congress would make the necessary appropriations to work up and publish all that he has brought together, not only on that cruise, but also what has been left untouched thus far of the immense collections made by him in the Caribbean, and off the east coast of the United States, to say nothing of his explorations in the Gulf of California, on the coast of California, on the coast of Alaska, and in the Behring Sea, from which he has accumulated endless and most interesting material, which no other ship could get together unless she had another Tanner in command.

We reached Guaymas on the 23d of April, in the afternoon, and I parted from the ship with great regret, but more than satisfied with the results of this expedition.

Allow me, in concluding, to thank you most cordially for having given me the opportunity to join the "Albatross" on this extended cruise, and for your kindness in urging the President to allow the vessel to be detailed for this work.

As soon as it may become practicable, I shall send you a full *résumé* of our work, accompanied with sketches of the Tanner tow-net and a detailed chart of the route we followed.

Very respectfully yours,

ALEXANDER AGASSIZ.

CAMBRIDGE, May, 1891.

No. 5. — *The Development of the Pronephros and Segmental Duct in Amphibia.* By Herbert H. Field.[1]

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I. Introduction.

The studies upon which this paper is based were undertaken with the purpose of determining the relation which the urogenital system bears to the germinal layers in Amphibia. At the time when they were begun, especial interest in this topic had been awakened by the appearance of Flemming's paper ('86), in which the author entirely confirmed the statement previously made by Graf Spee ('84), that the system was of ectodermal origin. This view was gladly welcomed on many sides, for it was felt that an origin from this source was more in harmony with general conclusions already accepted than was the method previously advocated. Moreover, a new light seemed now to be cast on the phylogeny of Vertebrates. Under these circumstances, it appeared highly desirable that the position which Graf Spee and Flemming had taken be subjected to the test of renewed investigation on other groups of Vertebrates than

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXVII.

those employed by them. The researches of these authors had been conducted on Mammalian material only, and it was the hope of the writer to find in Amphibia a similar mode of origin for the excretory duct.

The material employed in the present investigations consisted of embryos of Rana, Bufo, and Amblystoma. The study of the problem was begun with Rana pipiens Schreb. (halecina), embryos of which had been prepared in the spring of 1884 by Prof. E. L. Mark, who kindly placed his series at my disposal. In the spring of 1889, while in Baltimore, Md., I secured an abundance of the eggs of Rana sylvatica Le Conte.[1] These eggs are large, measuring at the blastula stage two millimeters or more in diameter. I also found them far better for embryological study than those of other species of frogs examined. An advantage which they possess for my purpose is that the germ layers are very well separated from one another. Moreover, the body cavity appears at an early stage, making the boundary between the somatic and the splanchnic mesoderm very pronounced, both in the region of the protovertebræ and of the lateral plates.

The eggs of Bufo studied, B. americanus Le Conte, were collected during the spring of 1887, in Cambridge and in Jamaica Plain, Mass. At this time I also collected a small quantity of Amblystoma eggs from a pond in Jamaica Plain; but a careful search, carried on during several subsequent trips to this locality, failed to yield any more eggs.

Prof. J. S. Kingsley at this time kindly sent me from Indiana some Amblystoma material which he had preserved; but for the determination of many points at issue I was obliged to wait till another season offered opportunities for collection. In the spring of 1889, therefore, I made a trip to Baltimore, where I was able to collect an abundant supply of the eggs of this Amphibian, most if not all of the material collected belonging to the species A. punctatum Linn. In this work I was accommodated at the Biological Laboratory of the Johns Hopkins University, — a privilege for which I am under obligation to that institution. My thanks are particularly due my friend Dr. T. H. Morgan for his kind assistance during my stay in Baltimore, and for material of his collection.

I may here also express my obligations to Dr. John S. Billings, Sur-

[1] Inasmuch as the observations of European investigators have usually been made on R. temporaria, it is of interest to note that R. sylvatica Le Conte has been regarded by some systematists as a variety of R. temporaria (Günther, '58, p. 17). In any event, the development of the two forms may be assumed to be very similar.

geon U. S. Army, for the favor of sending me from the Surgeon General's library in Washington a number of papers to which I should otherwise have been unable to gain access. I am further indebted to Mr. Samuel Garman and to Mr. G. H. Parker for the revision of my proof-sheets, and for suggestions during the progress of my work. Mr. Parker also read the earlier portions of my manuscript.

The material was prepared by ordinary histological methods; but inasmuch as many of the hardening reagents and stains which I tried gave thoroughly unsatisfactory results, I may state in brief the treatment which proved most successful. The embryos of both Rana and Bufo can be satisfactorily killed in Kleinenberg's picrosulphuric mixture; they can then be successfully stained in Orth's lithium-picrocarmin. The object should be exposed to the action of the stain as long as possible, care being taken to guard against maceration. In order to accomplish this purpose, it has frequently proved advantageous to stain the object twice, removing it after the first staining to strong alcohol. In passing the stained object through grades of alcohol, it is important to keep a little picric acid dissolved in the several fluids in order to prevent the alcohol from extracting the yellow stain from the specimen. Embryos treated in this way show a very effective double stain. The nuclei are bright carmine, contrasting with the yellow color imparted by the picric acid to the yolk spherules among which they are found. As a killing reagent, Merkel's fluid also gives good results. It should be followed by Kleinenberg's hæmatoxylin, and the decolorizing should be watched with care.

With Amblystoma the best method of treatment is that with Fol's chromic-osmic-acetic mixture, followed by Czokor's cochineal. The picrosulphuric mixture followed by picrocarmin, as recommended for Rana and Bufo, is also of service.

It is usually best to stain on the slide; and, in my experience, satisfactory results with hæmatoxylin can very rarely be reached by staining *in toto*.

II. Descriptive Part.

In the following account of the development of the pronephros and segmental duct, I shall first treat these organs descriptively. For this purpose, I shall take up in succession Rana, Bufo, and Amblystoma, and shall describe selected stages in the development of each. This account will be followed by a general discussion of nephridial organs, in which the results of other investigators will be reviewed.

A. Rana.

Stage I.

Plate I. Figs. 1-3.

At the first stage which I shall describe the embryo has departed only a little from the spheroidal form presented by the egg during segmentation. The medullary plate is widely open, its lateral margins being only slightly elevated above the general surface. At the hinder end of the medullary plate the blastopore is plainly visible. An idea of the external form of the embryo can be gained by reference to Goette's figure of Bombinator ('75, Taf. III. Fig. 41), or to van Bambeke's of the Axolotyl ('80, Pl. XII. Fig. 9). In water of 15 to 18° C. eggs of R. sylvatica reached this stage in about sixty hours after fertilization; the eggs of R. halecina develop somewhat more slowly.

The general relations of the germinal layers at this stage are shown in Figure 2. The ectoderm consists of two distinct layers (Figs. 3 and 7, *ec'drm.'* and *ec'drm.''*). Except in the region of the medullary thickening (*la. med.*), which is produced by a proliferation of the deeper of these two layers, the ectoderm is nearly uniform in thickness. The two layers present slightly different histological characters. In the outer layer (Figs. 3 and 7, *ec'drm.'*) the cells are large and columnar, and their external surfaces project as rounded eminences, giving a roughly granular appearance to the surface of the embryo. Each cell contains scattered pigment granules, which are especially massed along its external face. Small yolk spherules (*sph. vt.*) are present in considerable numbers. The cells of the deep layer (*ec'drm.''*) are smaller than those of the outer, and are somewhat flattened. The pigment granules are scattered throughout the cells of this layer, without showing special accumulations. The yolk spherules present the same appearance as those of the superficial layer.

The entoderm and yolk cells (Fig. 2, *en'drm.* and *cl. vt.*) form the great mass of the interior of the embryo. The wide lumen of the gut traverses the dorsal portion of this mass. The chorda (*n'cd.*) has the form of a longitudinal ridge, imperfectly cut off from the entoderm below, and in contact with the medullary plate above. A single cell layer (*en'drm.*) on each side of the chorda forms the dorsal roof of the intestine. As this layer passes out laterally, it increases in thickness, becomes several cells deep, and finally merges in the mass of large yolk cells (*cl. vt.*) lying ventral to the intestinal cavity. All the cells of the entoderm contain large yolk spherules. Pigment is present in considerable quantity in the

cells bordering the cavity of the intestine; elsewhere it occurs only as scattered granules.

At this stage two plates of mesoderm (Fig. 2, *la. ms'drm.*) extend out laterally, one on each side of the chorda, and pass ventrally around the mass of yolk cells to be united in the median line below. Each plate is thickest (Figs. 1, 3, at *la. pr'vr.*) next the notochord; as it passes outward, it becomes thinner. Before the ventral surface of the embryo is reached, it is reduced to a layer two cells thick, representing the somatopleure and splanchnopleure (*so'plu.* and *spl'plu.*) of this region. The cells of the mesoderm are in general smaller than those of the yolk-entoderm. The yolk spherules which they contain are also somewhat smaller than those in the entoderm. Pigment is rarely present except in the form of scattered granules.

In the foregoing account of the relations of the germ layers the description refers in the main to the typical condition, realized in the middle trunk region; in this and in subsequent stages modifications occur in the head and tail regions. These special conditions are of no consequence for the present purpose.

There are certain histological characters, to which allusion has already been made, which may serve as criteria for distinguishing the germ layers. The most satisfactory of these is the size of the yolk spherules. As I have indicated, the spherules are largest in the entoderm and smallest in the ectoderm; in the mesoderm they are of an intermediate size. Measurements of spherules from the three layers in the region of the future pronephros gave the following results: entoderm, mean diameter of spherules, $8\,\mu$; mesoderm, mean diameter, $5\,\mu$; ectoderm, diameter rarely exceeds $3\,\mu$. Excluding the head and tail regions, these dimensions represent, I believe, fair averages for the whole body. The distribution of pigment affords another criterion for distinguishing the layers. In the superficial ectoderm, the pigment (Figs. 3, 7) is massed along the external surface of each cell. In the deep ectoderm, it is present in considerable quantity, but is scattered throughout the cell. Except in certain specialized regions, there is little pigment in either mesoderm or entoderm. I have also noted the differences in the mean sizes of the cells: the yolk cells are in general the largest, and those of the ectoderm the smallest, the mesodermal cells being of intermediate size. The great variability of this character prevents its having much weight, however, in determining to which of the three layers a given group of cells belongs.

I shall now consider in greater detail some of the modifications which

the mesoderm exhibits, particularly such as occur in the region where the pronephros is subsequently developed. For this purpose I have selected two embryos of Stage I. which show slightly different conditions. The account will first relate to the specimen which is shown, by the less differentiation of the medullary plate as well as by other features, to be the younger. This embryo measures 2.31 mm. in length. In following a series of cross sections forwards, the three germ layers become apparent at about 0.35 mm. from the posterior end, or a short distance in front of the blastopore. Here the structure of the mesoderm is rather obscure, since in a transverse section of the animal this layer is cut obliquely. The condition, however, is here nearly the same as that which I am about to describe for a more anterior section.

Figure 3 represents a section of this embryo 0.91 mm. from the posterior end. On the ventral side of the embryo the mesoderm consists of two layers, each of which is only a single cell in thickness. These two layers, which represent somatopleure and splanchnopleure, are separated by a narrow space, the cœlom (*cœl.*). In the lower left-hand corner of the figure, the beginning of this two-layered condition of the mesoderm can be seen. On following the mesoderm towards the dorsum, it becomes gradually thicker. In the mesoderm of this region there is found an extensive cavity (*cœl.*), which is usually irregular in outline, and might be mistaken for a *wholly* artificial condition. That the two layers were once in contact is shown by the correspondence of outline on the two sides of the space. The separation along this line is so regular, however, in successive sections, and recurs so frequently in other embryos, that the cavity must be regarded as an artificial expansion of an already existing split, rather than as an indifferent rupture of a solid mass of cells. In many sections of this embryo it is easy to trace a line of division reaching from the ventral cavity (cœlom) to the large lateral cavity just described. This, then, represents a portion of the cœlom (normally, I believe, closed), and the layers of mesoderm on the two sides of it are consequently somatopleure and splanchnopleure. The mesoderm in this region, as I have stated, is several cells deep. Along the inner and outer edges of the wedge-shaped plate of tissue constituting the mesoderm of either side, the cells, except where artificial ruptures occur, are in close contact, and form an epithelial lamella. The central portion of the plate, where this is more than two cells in thickness, contains cells of a more rounded shape, which do not form definite rows, but which are closely applied to the outer layer, — a condition which becomes quite evident when the cœlom is artificially enlarged.

The somatopleure of this region, then, is a layer at least two cells in thickness. The splanchnopleure, on the other hand, in this as in later stages, consists of a layer one cell in depth, extending from the ventral surface of the animal to the protovertebral plate.[1] Naturally no sharp line of division can be drawn at this stage between the protovertebral plates and the adjacent portions of the lateral plates. In the section under consideration, the protovertebral plate is rather compact, and it is difficult to indicate with certainty the boundary between the somatic and splanchnic layers. A study of this portion of the mesoderm, however, has convinced me that the cœlom (*cœl.'*) is already outlined, and lies in such a position as to leave only a single layer of cells dorsal to it, — a condition which is perfectly evident in later stages. It is indicated by such a distribution of pigment as is seen to the right in Figure 3.

On following the series of sections farther towards the head, a constriction of the mesoderm appears beneath the lateral margin of the medullary plate, and the open cœlom is continued into the protovertebral plate. In a section 1.2 mm. from the posterior end the somatic and splanchnic layers are each but one cell thick in the region of the protovertebral plate. The cells of the somatic layer, which in the protovertebral portion are of a high columnar form, become tile-like beneath the pronounced lateral thickening (compare Fig. 1, *cras. gn.*) of the medullary plate. The somatopleure immediately lateral to the medullary plate is rather thick, and becomes thinner both towards the median dorsal and median ventral lines. The regularity of the bounding walls of the body cavity in this region, and the occurrence of a space where no other signs of distortion are apparent, lead me to believe that the separation of the two layers of mesoderm is here perfectly normal, and not, as in more posterior regions, an artificial separation of two closely applied lamellæ.

It is, in general, very difficult to observe karyokinetic conditions in mesodermal or yolk cells, owing to the presence of the large and numerous yolk spherules; but I am reasonably certain that I have observed cells in the somatopleural thickening, dividing in a plane parallel to the surface of the layer; i. e. the cells were dividing in such wise as to increase the thickness of the layer.

In a section 1.32 mm. in front of the posterior end, the lateral portion

[1] The differentiation of the protovertebræ has not yet begun in this region, and I shall designate the thick masses of mesoderm on each side of the chorda as protovertebral plates.

of the medullary plate is greatly thickened, and the lateral plates are thereby wholly cut off from the protovertebral plate. The thickening of the medullary plate is the hinder portion of a considerable ganglionic mass, which is the basis for the subsequently differentiated ganglia Gasseri, acusticum, and nodosum.[1] The somatopleural thickening may be traced to a point about 80 μ farther forward, where the body cavity is no longer expanded. The relations of this thickening to the nephridial organs will be discussed in connection with Stage II. (page 211).

In a slightly older embryo, measuring 2.34 mm. in length, the condition of the mesoderm is nearly the same as in the one last described. The somatic layer shows a marked thickening (Plate I. Fig. 1, *cras. so'plu.*), which is greatest immediately lateral to the protovertebral plate. An anterior cœlomic chamber is also present. The anterior limit of the thickening is situated, as before, about 0.1 mm. in front of the hinder end of the enlargement which is destined to give rise to the cranial ganglia. The thickening (Fig. 1, *cras. so'plu.*) of the somatopleure is slightly more pronounced than in the younger embryo.

The results of this study may be summarized as follows. There exists already at this stage a slight somatopleural thickening, which is maximum along a line immediately lateral to the protovertebral plate. This thickening is associated with a local expansion of the cœlom. It is most pronounced in the region directly posterior to the cranial ganglionic mass. Posteriorly it is lost in a general lateral thickening of the somatic layer. The location of the thickening corresponds closely with the region in which the pronephros and segmental duct later arise. Whether we have in this thickening the first rudiment of the excretory system will be discussed in connection with Stage II.

[1] I may here note that I have been able to make out for the series of spinal and cranial ganglia in Rana, Bufo, and Amblystoma an origin not unlike that described by Beard ('88, pp 166, 183) in Selachii and Aves, and by Schultze ('88, p. 349) in Rana. The ganglia are developed from the ectoderm at the lateral margins of the medullay plate (Fig 3, *fnd. gn. spi.*). The differentiation of the ganglia is already apparent before the neural tube is infolded A spinal ganglion does not arise as an outgrowth from the neural tube, nor as a separate thickening of indifferent ectoderm, but is differentiated from a first rudiment (Anlage) common to it and to the neural tube.

Stage II.

Plate I. Figs. 4, 5. Plate II. Figs. 13, 14.

This stage includes embryos with a distinct medullary groove, the edges of which, however, have not yet fused to form a complete neural tube. Several protovertebræ can be distinguished.

In treating of the structure of the pronephros in this stage I shall first consider two embryos, which, judging from external appearances, seem to have reached the same stage of development. These embryos are about as far advanced as the one figured by Hertwig ('83, Taf. V. Fig. 6). In both the medullary groove is widely open. They are about 2.5 mm. long, and have been sectioned, one transversely, the other frontally.

Following the series of cross sections forward from the tail end, and comparing them with those of the preceding stage, the changes which have occurred will be apparent. In the posterior region, the mesoderm, as it passes outward and downward from the chorda, tapers much more rapidly than in the earlier stage. Even as far posteriorly as a few sections in front of the blastopore, this condition can be observed; and, in a section 0.72 mm. from the posterior end, the thick central mass of mesoderm, the protovertebral region (Fig. 4, *la. pr'vr.*), has a triangular outline in cross section, and is readily distinguishable from the lateral plate (*la. l.*), with which it is continuous at its outer angle. The protovertebral plate consists of an outer epithelial layer and a central mass of cells. It is the former which is prolonged into the lateral plates. Each of these is here in general only one cell deep. Between somatopleure and splanchnopleure a few scattered cells occur, which can be assigned only with difficulty to either layer.

At 0.96 mm. from the posterior end the hindermost protovertebra visible in cross section can be distinguished. Between this point and the ganglion nodosum four protovertebræ are to be observed. Passing farther forward, it is difficult to assign boundaries to the protovertebræ. There is certainly one which is partially broken up into mesenchymatic tissue.[1] Still farther forward the series of the protovertebræ is continued by mesenchyme of a yet looser structure. Inasmuch as I have

[1] I use this expression merely as descriptive of tissue of a certain histological character, quite independently of its origin. Indeed I am convinced, from observations which appear in the sequel, that not merely the head mesenchyme, but also much of that in the trunk, arises in relatively late stages from mesodermal tissue, substantially in accordance with the account of Balfour ('78, pp. 107 *et seq.*), which has recently found champions in Ziegler ('88) and others.

reached no conclusions respecting the number and position of the head somites, and since great diversity of opinion exists in the accounts to be found in the literature, I shall make no attempt to number the protovertebræ with which I shall have to do in any other way than by beginning with the most anterior that is readily distinguishable. Disregarding, then, the one which is wholly broken up into mesenchymatic tisue, somite I. lies in the same transverse plane as the fundament[1] of the ganglion nodosum, and extends backward to the hinder end of that structure. This protovertebra also shows signs of extensive conversion into mesenchyme, although part of it at a later stage undergoes muscular differentiation. Somite II. is the first of the series of well developed trunk protovertebræ. In the specimen under consideration somites I. to VI. are already differentiated.

As I have stated, the somatopleure in the middle of the trunk consists of a layer one cell deep, to which a few loose cells lying between it and the splanchnopleure may possibly also be assigned. In the region of somite IV. the somatopleure becomes thickened. The thickening is greatest at the level of the lower margins of the protovertebræ (compare Plate II. Figs. 15, 16), and tapers both dorsally and ventrally. It is to be remarked in this connection that the protovertebræ are not yet fully separated from the lateral plates; but that in cross sections through the middle of a somite, — i. e. midway between the anterior and posterior faces of a protovertebra, — the cœlom can be traced to the dorsal margin of the protovertebra, and furthermore that the somatopleure and splanchnopleure are seen to be continuous with the somatic and splanchnic layers of the protovertebræ. The somatopleural proliferation extends forward as far as the anterior face of somite II. The cells in the thickening have a columnar shape, and are at least two deep. In some sections I have observed, in addition, a third row of thin cells next the body cavity. Near the ventral limit of the thickening a nearly horizontal line of division in the substance of the thickening can be observed. When seen in cross section, this line is slightly concave above. It is here that ruptures produced by artificial causes are likely to occur, and the line thus indicated marks, I believe, the lower limit of the pronephros. The somatopleural thickening is the fundament of the pronephros, and I shall call it in the following pages the

[1] In the following pages I shall use the word *fundament* as an equivalent of the German expression *Anlage*, the term *fundamentum* having been adopted as the basis for the lettering of the figures of such structures in the "Contributions" from this Laboratory.

pronephric thickening. The dorsal portion of the expanded body cavity is the pronephric chamber.

The question whether the somatopleural thickening described in Stage I. be an early condition of the pronephric thickening is only to be answered by considering the fate of the former. Behind somite IV. this early thickening wholly disappears, and the one which is seen at a later stage is an independent formation. This conclusion is justified by a comparison of Figure 4 (Plate I.), showing the somatic layer to be only one cell thick in the posterior region of an embryo of the present stage, with Figure 3, which shows a two to three layered somatopleure (*so'plu.*) in a somewhat more anterior region of an embryo of the next younger stage. In the region of somites II., III., and IV., however, the somatopleure never wholly thins out; but the thickening is here moulded into a more definite form, and becomes the fundament of the pronephros. To my mind, it is as if the mesoderm, in the process of becoming thinner, was overtaken by the necessity of affording material for the formation of the pronephros and duct, and, as a matter of physiological economy, used for that purpose an accumulation of cells already present. Indeed, from the form of the thickening in anterior portions of the embryo, I am disposed to regard the differentiation of the pronephric thickening in this sense as having begun already in Stage I.

The corresponding series of frontal sections shows five well developed protovertebræ, representing somites I.–V. (Plate II. Figs. 13, 14). A mass of mesenchymatic tissue in front of somite I. is doubtless the remnant of the rudimentary anterior protovertebra observed in the series of cross sections, and behind somite V. the differentiation of a sixth is faintly indicated. Above the level of the lower border of the chorda the protovertebræ are sharply marked off from one another, and the somatic layer is relatively thin. Near their ventral margins, however, the successive protovertebræ are in close contact, and the somatic layer shows a pronounced lateral thickening (Fig. 13, *cras. pr'nph.*).

On passing ventrally to the region of the lateral plates, the interprotovertebral constrictions vanish. Since frontal sections, however, do not here cut the layer of mesoderm perpendicularly, certain sections in the series show a distinctly segmented splanchnic layer, while the somatic thickening in the same frontal plane is unsegmented. Farther ventral there are no traces of segmentation in either layer. Here the splanchnopleure (*spl'plu.*) uniformly consists of a single layer throughout its entire extent. The somatopleure facing the ganglion nodosum, and also that in the posterior region, is thin; but in the anterior portion of

the trunk, immediately behind the ganglion nodosum, there is a marked thickening (*cras. pr'nph.*), which ends abruptly in front, but gradually thins out into indifferent somatopleure behind. This thickening is distinctly present through a length of 0.5 mm., which is slightly greater than the extent of protovertebræ II., III., and IV. Still farther ventrally, the antero-posterior extent of the thickening is much diminished, the reduction taking place from both ends, so that in passing ventrally the region in which the structure is last visible is situated approximately beneath protovertebra III.

Another pair of embryos, one of which was 2.5, the other 2.6 mm. in length, presented a condition of the pronephros somewhat more advanced than that just described (Plate I. Fig. 5). In these embryos the lips of the medullary fold in the most advanced region were in contact, but had not yet fused. The anterior limit of the pronephric thickening was the same in position as in the younger pair of embryos, lying near the middle of somite II. A study of the arrangement of the nuclei in this region made it evident that there were at this stage in general three layers in the thickening. The innermost of these is the thinnest, and is destined to become the peritoneal covering of the pronephros; the other two represent the two walls of the pronephric pouch, soon to be described. The pronephric thickening in the region of the anterior face of somite IV. is shown in Figure 5. The section gives a somewhat false impression as to the somatic layer of the protovertebra, unless the relation of the section to the successive somites be borne in mind. The considerable thickening which this layer apparently undergoes on passing into the protovertebra is due to the circumstance that the section here passes obliquely through a portion of the anterior wall of somite IV. Sections through the middle of a protovertebra show a gradual thinning of the somatic layer as far as the dorsal angle of the mesoderm (compare Plate II. Fig. 15, which is a cross section of the following stage), where this layer is almost pavement-like. The pronephric thickening extends rather farther posteriorly than in the former pair of embryos, and while it is manifestly difficult to set a limit to the structure, I am confident that the thickening extends into somite V. This posterior extension of the thickening is to be regarded as the fundament of the *pronephric*, or, according to the later nomenclature of Balfour, the *segmental duct*.

The corresponding series of frontal sections shows six well differentiated protovertebræ, representing somites I.–VI. The same group of cells which I interpreted before as the last remnant of a rudimentary

anterior somite is still present, and a few more posterior protovertebræ are in process of formation. Frontal sections just ventral to the chorda are very instructive. By following through a series of these, an idea can be had of the successive changes which take place in passing from the protovertebræ to the lateral plates, — a region of prime importance for problems respecting the development of the urogenital organs. In sections approximately tangent to the chorda at its ventral border (compare Fig. 5), the plane of the section passes through the ventral floor of the protovertebra, and cuts the somatic mesoderm near the place where the protovertebra passes into the lateral plate. The body cavity is expanded in the anterior part of the trunk. The mass of tissue on the median side of the body cavity appears very broad, owing to the circumstance that the plane of the section, as before noted, lies in the floor of the protovertebra. The somatic layer is several cells thick, and very compact in structure, owing to the fact that the section passes through the dorsal margin of the pronephric thickening. In following the series of sections farther ventrally, the boundaries between the segmental constituents of the pronephric thickening become indistinct; and in a section 90 μ farther ventral they have wholly vanished. This section, however, still shows traces of segmentation in the splanchnic layer, which is here reduced in thickness, the plane of this section having passed ventral to the floor of the protovertebra. Still farther ventrally the segmentation of the splanchnopleure likewise vanishes, and finally the pronephric thickening gives place to undifferentiated somatopleure. I have looked in vain for prolongations of the body cavity into the pronephric mass at this stage. I believe that the pronephric thickening is to be regarded as a solid proliferation of the somatopleure, in which, however, the somatic layer of the protovertebræ takes some part.

Stage III.

Plate I. Fig. 6. Plate II. Figs. 11, 12, 15-17.

In embryos of this stage the medullary canal is wholly closed, the fundaments of two pairs of gills are present, and the auditory vesicle consists of a shallow depression of the deep ectoderm.

The pronephric thickening has now begun to assume a more definite form, and during this stage becomes converted into a tubular organ. I shall first consider the structure as seen in a series of cross sections from an embryo measuring about 2.7 mm. in length. Figures 15 to 17 are from this series. The anterior end of the pronephric thickening is

located in somite II. The plane of the section from which Figure 15 was drawn passes somewhat behind the middle of this somite, so as to show the location of the constriction between the protovertebræ and the lateral plates. In the middle of the somite, the arrangement of the cells composing the pronephric thickening appears to be that of a fold in which the layers are in close contact. The thickening is composed of three layers of cells, and it is possible to trace the somatic layer of the protovertebra into the outer layer of the thickening. The lateral indifferent somatopleure is continuous at the ventral border of the thickening with the inner or thin layer which lies next to the body cavity. Near the upper border of the thickening this inner layer appears to be folded abruptly on itself to form the middle layer of the thickening. The middle and outer layers are continuous with each other distally, i. e. ventrally.[1] This anterior knob of the pronephric thickening (Fig. 15, *fnd. nph'st.*[1]) is the fundament of the first nephrostome, a later stage in the development of which is shown in Plate III. Fig. 18 (*nph'stm.*[1]). In Figure 15 the three layers are indicated by the arrangement of the nuclei. Of these the two outer form the fundament of the first nephrostomal tubule. The innermost layer represents the underlying peritoneum. In the region between somites II. and III., it is impossible to distinguish definite layers in the thickening.

On entering somite III., the pronephric thickening has a far greater breadth, and it consists of three layers, the meaning of which is to be understood by a comparison with the condition in the region of the first nephrostome, just described.

In somite IV. (Fig. 16) a division of the thickening into a dorsal and ventral part is indicated, near the termination of the dotted line (*cras. pr'nph.*). The dorsal part is the fundament of the third nephrostome, and the ventral part represents the anterior portion of the segmental duct (more properly, common trunk, see page 228). The ventral portion of the thickening can be traced backwards from this point through a distance of about 0.37 mm. Figure 17 is drawn from a section through a region near the anterior boundary of somite VII., and shows

[1] The correlative terms *distal* and *proximal* are so frequently employed by German writers as synonymous respectively with *posterior* and *anterior* that it seems advisable to allude to the fact that they are not used in the present paper in that sense, but invariably with their primitive signification; thus, the distal portion of a process is that part which is most remote from the point of attachment, whether the structure project anteriorly or posteriorly, medially or laterally, dorsally or ventrally.

the thickening (*cras. pr'nph.*) near its posterior termination. The mass is evidently a thickening *in situ* of the somatopleure. On either side of the fundament of the segmental duct the somatopleure is one cell thick, whereas in the fundament itself it is two or three cells in thickness. If the additional cells arose by a free backward growth from the anterior pronephric mass, we should expect to find them lying on the external face of a continuous somatopleural layer. But, as a matter of fact, no such continuous inner layer exists; on reaching the thickened region, the somatopleure merely becomes several cells in thickness, the outer cells presenting really a somewhat more compact condition and a more linear arrangement than the inner ones.

The constrictions between the protovertebræ and the lateral mesoderm can be distinctly made out only in intersegmental regions. As is shown in Figure 15, between somites II. and III. the level of the constriction is immediately dorsal to the nephrostomal portion of the pronephric mass. In the region between somites III. and IV. the division occurs at a corresponding position. This series of sections shows no sharp separation between protovertebral and lateral mesoderm posterior to somite IV., the protovertebral plate being here only partly broken up into successive metameric blocks, which do not as yet possess sharp ventral boundaries.

In frontal sections, the pronephric thickening shows a similar condition (compare Figs. 11–14) to that which obtains in the case of the embryo described under Stage II. (page 213), the most noticeable difference being an increase in the thickness of the pronephric mass. The longitudinal extent of the thickening corresponds approximately to that of five somites, though the posterior limit is of necessity somewhat uncertain. The posterior portion has every appearance of having arisen in the same way as the part lying beneath somites II., III., and IV. The latter, however, represents, as we have seen, the future pronephros; the former is the fundament of the segmental duct.

In an embryo slightly older than those last described, the evidences of an incipient canalization of the pronephric system are more pronounced. In the region of somites II.–IV., the two outer layers of the pronephric thickening are separated from the peritoneal layer by a distinct line of division. In the intersegmental regions, the outline of these two layers is that of an elongated ellipse, the nuclei being disposed, for the most part alternately, on either side of its major axis. The significance of this distribution becomes apparent on studying later stages, in which a lumen

has appeared in the organ. It is then found that the lumen occupies the position of the major axis of the ellipse, and that the nuclei of the bounding cells lie close to the interior surface of the wall. If a tube so constituted be compressed laterally, so that the lumen wholly disappears, it is evident that the cells of the opposed walls would be likely to accommodate themselves to one another so as to present an alternate arrangement of their nuclei.

Opposite the middle of a somite, the relations are somewhat different. Here the two layers of what I shall hereafter call the pronephric pouch do not remain confluent at its dorsal extremity, but separate, the outer becoming continuous with the somatic layer of the protovertebra, the inner with the deepest layer of the thickening, and thus finally with the lateral somatopleure. In this region the body cavity can be seen to project for a short distance between the two layers of the pronephric pouch, as shown in Plate I. Fig. 6, *cœl*. This figure demonstrates very clearly the relations of the pouch to the lateral mesoderm and the overlying somites.

In the case of the younger set of embryos which have been considered in this stage, it will be remembered that the boundary between the lateral mesoderm and the protovertebræ was evident only in intersegmental regions. In the somewhat older individual now under consideration, the constrictions between these two portions of mesoderm have advanced into segmental regions as well; so that now, for the first time, the precise relations between the fundaments of the nephrostomes and the protovertebræ lying above them can be accurately determined. The last remnant of the communication between the protovertebral cavity and the body cavity I shall call the communicating canal, following in this the nomenclature of Renson ('83). The section shown in Figure 6 passes through this canal (*can. comm.*), and it is to be especially noted that the constriction between the somites and the lateral plates takes place dorsal to the region of communication between the pronephric system and the body cavity. Immediately dorsal to the pronephros, the somite sends out a lateral fold of the somatic layer, which is destined to form the capsule of the pronephros, to which I shall have occasion to refer in later stages.

In somite IV., the division of the pronephric mass into a dorsal and ventral part is faintly indicated, but the dorsal part shows no trace of the lumen which is destined to become the third nephrostome. In this embryo, the constrictions between the protovertebræ and lateral plate have advanced into more posterior regions. In somite V. the constric-

tion occurs immediately dorsal to the fundament of the segmental duct, which, as I have shown, is continuous anteriorly with the ventral half of the thickening appearing in somite IV. A series of measurements from the dorsal median line shows that the ventral portion of the pronephric thickening remains at a nearly constant level, so that the protovertebræ must reach a somewhat more ventral position in the posterior region than in somites II.–IV.

Figure 11 (Plate II.) represents a frontal section through the dorsal part of the pronephric pouch in one of the oldest embryos of this stage. It shows the course of the earliest fundaments of the three tubules which emerge from the somatopleure beneath protovertebræ II., III., and IV. The most anterior outgrowth, arising in somite II., inclines outward and backward into the region of somite III.; the second outgrowth proceeds from its origin beneath protovertebra III. directly outward; and the third outgrowth inclines forward, so that its distal extremity also lies in the region of somite III. As the review of the previous stages has shown, these fundaments of the tubules have *not arisen as separate outgrowths* from the somatopleure, but have been differentiated from the originally continuous pronephric thickening, the three fundaments being confluent distally.

In this section the nuclei are abundant along a central band, but scarce or wholly absent in peripheral parts. This peculiar arrangement becomes intelligible when we consider that the plane of the section passes almost tangentially through the curved dorsal wall of the pouch. As we have seen in transverse sections, the nuclei lie close to the inner lumen of the pouch; it is therefore only in the deeper central parts of the section that they are encountered. In a section 0.03 mm. farther ventral (Fig. 12), the lumen of the pouch can be made out, though it is not conspicuous. It is difficult to say whether at this stage the lumen is continuous throughout the whole structure. In many embryos the evidence of such continuity seems indubitable; whereas in others, apparently quite as far advanced in other respects, the lumen seems to consist of unconnected portions. In some instances where no trace of a separation of the walls could be seen, a line of pigment indicated the position of the lumen. Occasionally I have met with a distinct prolongation of the body cavity into the pronephric mass. This condition has been most frequently encountered in the case of the fundament of the first tubule. I am not, however, inclined to place much weight on such observations as proving the claim that the lumen of the pronephros forms as an ingrowth of the cœlom proceeding from the nephrostomes and advancing into the duct.

On the contrary, the lumen is already potentially present, as shown by the arrangement of the nuclei before any actual separation of the walls occurs. I am of opinion that, in the cases referred to, the separation is largely artificial, and that the ruptures take place most frequently at the nephrostomes for the reason that the walls, which elsewhere form a closed ring, here have in cross section the form of a sharp re-entrant angle bordering on a large open space. It is evident that in the former region the walls would be less liable to be torn apart in the preparation of the material than in the latter. In general, however, it must be admitted that the development of the lumen, like that of the system as a whole, actually advances from anterior to posterior regions.

The fundaments of the three pronephric tubules shown in Figure 11 are not to be regarded as outgrowths from the somites. They are, it is true, very closely related to the segments in their arrangement, but, as transverse sections prove (Plate I. Fig. 6, and Plate II. Fig. 15), they lie wholly ventral to the lower boundaries of the protovertebræ. The frontal section figured (Fig. 12) was chosen for the reason that it was the one which indicated most precisely the course of the fundaments of the three tubules. The plane of the section is parallel to a tangent to the dorsal margin of the structure, and passes only a little below that margin, not through the nephrostomes. These begin in a more ventral unsegmented region.

In the oldest embryos of this stage, the fundament of the duct has developed very rapidly. Anteriorly, it has in cross section a distinctly elliptical outline, and its cells have, with reference to the major axis of the ellipse, the same arrangement that I have described for the intersegmental regions of the pronephric pouch. On following the structure backwards, this distribution becomes less and less obvious, until the cells seem to have no definite arrangement. In this region the fundament of the duct is in far more intimate union with the somatopleure than was the case in anterior somites. In the region of somite IX. the last trace of the structure is to be seen as a simple thickening of the somatopleure, similar in form to that described and figured in the youngest embryos of this stage (Fig. 17), for a region just back of somite VI. The region in which the duct is formed is throughout immediately ventral to the constriction separating the protovertebræ from the lateral plates.[1]

[1] In sections from the posterior end of the embryo, it is necessary to guard against the false appearances which arise from the obliquity of the plane of the

The mode of development which I have described in the foregoing pages, taken in connection with frontal sections, which show that the pronephric thickening tapers gradually backwards into indifferent somatopleure, seems to me to be very strong evidence concerning the precise origin of the duct. I believe I am justified in concluding that *the segmental duct between somites V. and IX. arises in situ from a thickening of the somatopleure serially equivalent to that from which in the anterior region the pronephros is developed.* Indirect evidence which can be brought to bear on this question will be reserved for the fuller consideration which can be accorded it, in connection with the following stage (page 222).

Stage IV.

Plate I. Figs. 8, 9. Plate III. Figs. 18-26. Plate IV. Figs. 29, 39. Plate V. Fig. 45.

I have placed in this stage embryos of frogs taken from five different killings. They all belong to the fourth day after fertilization, and aside from individual variation show an evident advance in organization on the preceding stage. In all a distinct differentiation of muscular tissue has begun, the auditory vesicle is wholly cut off from the epidermis, and the ventral sucking (or more properly sticking) disks are well developed. In the following description, I shall find it convenient to distinguish a younger and an older set of embryos. In the younger set the embryos are from $3\frac{1}{4}$ to $3\frac{1}{2}$ mm. long; they have about 14 protovertebræ and the fundaments of 3 pairs of gills. The embryos of the older set are from $3\frac{1}{2}$ to $3\frac{3}{4}$ mm. long; they possess about 17 protovertebræ and the fundaments of 4 pairs of gills.

All the embryos of this stage have the pronephric pouch in its typical form. A side view of this organ with the neighboring portion of the

section to the vertical axis of the protovertebra. Cross sections in this region frequently encounter two contiguous protovertebræ. If the plane of the section traverse the communicating canal of a protovertebra, it would also pass obliquely through the dorsal portion of the next anterior protovertebra. The latter would then appear in cross section as a distinct mass immediately lateral to the neural tube and the chorda, and would resemble the condition which a protovertebra presents when cut near its anterior or posterior wall. Immediately below this mass there would be found on the same cross section the ventral portion of the more posterior protovertebra, with the corresponding part of its cavity. The latter, however, being apparently a direct continuation of the body cavity, owing to the existence of the communicating canal, would appear to represent the dorsal part of the body cavity, and the fundament of the duct would thus seem to be farther removed from the dorsal angle of the body cavity than it really is.

segmental duct is shown in Figure 39 (Plate IV.). In this drawing, the outlines were obtained by reconstruction from a series of cross sections. The pronephric pouch is suspended from the dorsal angle of the body cavity by the nephrostomal funnels. Elsewhere it is wholly cut off from the mesoderm, and merely rests conformably on the outer surface of the somatopleure. The precise relations of the parts can be understood by referring to the series of cross sections shown in Figures 18 to 22 (Plate III.). Figure 18 represents a section through the left pronephros in the region of the first nephrostome. The location of the plane of this section in the reconstruction is indicated by the dotted line *18*, in Figure 39. The lateral plates are here wholly cut off from the protovertebræ, splanchnopleure and somatopleure being continuous with each other at the dorsal angle of the body cavity. Figure 19 shows the structure of the organ between the first and second nephrostomes. In this and the following sections it was found advisable to depict the pronephric structures of the *right* side in order to exhibit in each case the section which most clearly showed the structural conditions. The next drawing (Fig. 20) in the series represents a section through the second nephrostome. In the preceding section, — not figured, — the three portions into which the lumen is here divided are continuous. The constriction between the middle and the ventral lumen is artificial; for the cells occasioning this local closure do not belong to the proper wall of the pouch, but form a group within the cavity. In several instances I have observed such groups of cells lying entirely free in the lumen of the pouch (Plate V. Fig. 45). In the present case, however, the mass is very intimately connected with the adjoining walls. This condition is preserved through a distance corresponding to the thickness of two or three sections, but the mass terminates by becoming free from both walls, so that in cross section it has the appearance of an "island" of tissue occupying the lumen of the pocket. The occurrence of these islands within the cavity of the pouch is of significance in determining precisely how the organ is developed. It is difficult to comprehend how they could be formed, provided the canals were produced by a fold of the somatopleure. On the other hand, they are perfectly intelligible on the assumption that the canals arise by the rearrangement of a solid mass of cells into a peripheral layer with a central lumen. According to the latter view, the islands would represent residual portions of the pronephric thickening which had not been transformed into peripheral wall.

Returning now to the section last under consideration (Fig. 20), the

ventral union of the walls of the pronephric cavity is, as I have shown, artificial; the constriction between the middle portion of the lumen and the dorsal, or nephrostomal, portion is more apparent than real, for it is formed by the posterior wall of the nephrostomal tube, the plane of the section not having cut exactly in the axis of the tubule. In the section following that shown in Figure 20, the pouch is detached from the peritoneum, and presents an appearance similar to that shown in Figure 19. Before the third nephrostome is reached, the canal is divided by a horizontal constriction into two tubes. The dorsal portion forms the tubule of the third nephrostome; the ventral portion is the anterior end of the segmental duct. Figure 21 shows these parts in the region of the third nephrostome. The section corresponds in position with the dotted line *21* in Figure 39.

In the following sections the duct rapidly assumes a more dorsal position (compare Fig. 39). It then proceeds directly backward, at the level of the constriction between protovertebræ and lateral plate. Figure 22 shows the duct in the region of somite VI. It has not yet been formed, however, throughout its entire length. On passing posteriorly, it gradually loses its lumen; then the circular arrangement of the nuclei indicating the position of the lumen also vanishes; the structure at length terminates as a simple thickening of somatopleure in the region of the tenth somite. In a few individuals, however, I found slight evidences of a mode of ending different from that just described. In one case the indications seemed so strong as to compel me to seek confirmation of the view that the duct takes its origin *in situ*. I shall therefore give the details of the evidence on this point, and discuss its probable significance.

Figure 23 represents in cross section the fundament of the duct in this specimen, as shown in the fifth section in front of its termination. The section of the mass here contains about eight cells, which are in close contact with the somatopleure. In the second section behind this one there are shown parts of four or five cells (Fig. 24). The protoplasmic patch in the centre (*cd.*) is wider than an average cell of the fundament, and probably represents the anterior ends of two cells lying in the following section (Fig. 25, *c.* and *d.*). Dorsal to this mass of protoplasm is a nucleated cell (*b.*), and above this a small area of protoplasm with a faint nucleus (*a.*) which is doubtless a portion of a cell the principal part of which was cut off by the preceding section. On the ventral side of the centre of the fundament there is also a round nucleated cell (*e.*). In the next following section (Fig. 25), there are two nucleated cells in the

centre of the mass (*c.* and *d.*), which, as I have said, doubtless correspond to the central protoplasmic area (*cd.*) seen in the preceding section. The most prominent cells of that section are here represented by two faint circles of protoplasm (*b.* and *e.*). In the next following section, not figured, the duct terminates as a single non-nucleated mass, probably corresponding to the dorsal cell in Figure 25. This remnant lies in a distinct depression of the somatopleure (Fig. 26, *f.*). This depression continues backwards through the space of three sections. Instead, then, of terminating in a thickening of the somatopleure, the end of the duct lies in a groove of unmodified somatopleure. There is no tissue directly behind the duct for its further growth, and the inference is natural that the somatopleure is mechanically depressed before the growing tip of the duct. In fact, I believe this to be actually the case, and that in this region the duct does grow by a simple cell proliferation within its own mass.

The key to the situation is to be found in the location of the posterior end of the duct in this specimen. An enumeration of the somites shows that the sections figured lie at the hinder end of somite XI. To show the bearing of this fact, I shall anticipate some of the results of a study of Stage V. In a series of frontal sections of the latter stage, I have succeeded in locating with reference to the successive somites the position at which the duct opens into the cloaca. The openings are in the same vertical plane with the middle of somite XII. The posterior end of the duct, then, in the specimen which I have just described, is within the distance of half a somite from its final termination. In order to empty into the cloaca, the duct has to grow inward from its position at the lateral margins of the protovertebræ to a position much nearer the median plane. It is difficult to comprehend how the duct could make this extension, except by proliferation of its own cells. It is just in this region that I find evidences of such a mode of growth. If the inference I have drawn from the facts adduced be correct, it seems to me to add strength to the conclusion I have reached in regard to the general mode of formation of the duct, inasmuch as it has been shown to be possible to detect free growth where it exists.

That the duct arises in the way I have described, and is not developed from the ectoderm, is shown, moreover, by certain indirect evidence which may be properly discussed at this point. As I have already stated, the duct is developed in such intimate connection with the somatopleure that I have been led to believe that it arises throughout its entire length from a proliferation *in situ* of that layer. In almost all of my prepa-

rations the duct in its backward growth is separated by a considerable space from the ectoderm, and I have observed no instance in which it was impossible to distinguish a perfectly sharp line between the fundament of the duct and the overlying ectoderm.

In describing the germ layers in Stage I., I referred to certain histological criteria which might be employed in determining to which germ layer a given group of cells belonged. The most valuable of these is the difference in the size and abundance of the yolk spherules, which even in that early stage served to contrast sharply the mesoderm from the ectoderm. In later stages, this character is equally pronounced. When the duct appears, the cells which constitute it are not distinguishable in histological features from those of the adjacent mesoderm, but are very different from those of the neighboring ectoderm. It seems to me extremely improbable that the cells of the fundament of the duct, with their numerous large yolk spherules, should have been recently derived from those of the ectoderm, which are provided with only few spherules of much smaller size. It would be entirely contrary to our conceptions of the physiological nature of yolk, if in the course of embryonic development this material was increased instead of diminished in quantity.

A similar argument seems to me to afford evidence that the duct arises *in situ*. If the duct had grown freely backward from an anterior proliferation, such growth would in all probability have been associated with the consumption of yolk in the cells of the fundament, and the spherules would be smaller or less numerous than those of the adjacent mesodermal cells. This, however, is not the case.

I conclude, therefore, that the segmental duct arises throughout its entire length by a proliferation *in situ* of the somatopleure. Its posterior end, however, grows across to the cloaca free from adjacent tissue.

Returning to the pronephric pouch, I purpose describing the relations of that organ to the somites. The section represented in Figure 29 (Plate IV.) shows graphically these relations. The plane of section in this case was very nearly tangential to the somatopleure at the points where the nephrostomes emerge. In this section it is evident that the three nephrostomes lie precisely under the first, second, and third somites, behind the ganglion nodosum. These correspond to the somites which I have numbered II., III., and IV.; so that the pronephric pouch remains in the same position as the pronephric thickening of earlier stages. In Figure 21 (Plate III.) the last remnant of the canal connecting the body cavity with the cavity of the protovertebræ is faintly indicated (above the letters *cœl.''*) in the same transverse

plane as the third nephrostome; and Figure 6, as we have seen, shows more plainly the same condition in the case of the second nephrostome at an earlier stage.

The structure of the protovertebræ in this stage (Plate V. Fig. 45) merits especial consideration. Already in younger stages there is a differentiation of a peripheral epithelial layer surrounding the dense central mass, or kernel of the protovertebra. Laterally this peripheral part is represented by the entire somatic layer, which is separated from the kernel by the protovertebral cavity (*cœl.*). Along the median and ventral boundaries of the somite, a layer having an epithelial character is also to be seen. Thus the central mass which is to develop into the myotome lies on the median side of the cœlom, and is wholly surrounded by an epithelial layer. Frontal sections show that this layer can be traced inward for some distance between successive somites, both from their median and lateral surfaces. Since the development of the protovertebræ proceeds from before backwards, a single frontal section shows successive stages in the changes which they undergo. From such a section it is apparent that neither the median nor the lateral portion of the peripheral layer develops muscular fibres. That portion of this layer, however, which is included between the kernels of successive protovertebræ, is apparently differentiated into muscle, and becomes merged in the myotomes. Very soon after the first development of muscle fibres in the myotomes, the peripheral portions which have not been converted into muscle separate from the central mass, and, while yet adhering in a lamella, show evident signs of disassociation. It is to be noted, that, in regions where traces of the communicating canal are still distinguishable, the median peripheral layer, not the kernel, is seen to be continuous with the splanchnopleure. The somatopleure, on the other hand, may be traced, as before, into the outer layer of the protovertebra. This peripheral layer I believe to be wholly converted, with the exception stated, into mesenchymatic tissue. In the stage before us we see that it is distinctly breaking away from the myotome, and that the cells are acquiring a flat tile-like form. In the following stage no layer that could properly be called epithelial is present. In its stead there is a considerable quantity of loose mesenchyme, and the lateral face of the myotome is covered by a sheath consisting of very delicate fibrillar connective tissue.

Not merely is mesenchyme produced by the thin peripheral layer of the protovertebræ, but in anterior regions considerable portions of the kernels of the protovertebræ also undergo a metamorphosis in this direc-

tion. Thus, if I be not mistaken, a protovertebra immediately in front of somite I. has been wholly converted into mesenchymatic tissue; the kernel of the succeeding protovertebra (somite I.) has given rise to a considerable quantity of mesenchyme; and the process has been manifested, though to a less degree, even in succeeding somites. Furthermore, having established the continuity of splanchnopleure and somatopleure with the median and lateral peripheral layers respectively of the protovertebræ, it seems to me the more probable that the former as well as the latter may give rise to mesenchyme. I have, in fact, seen conditions directly in front of the first nephrostome which indicated a very extensive production of mesenchyme from the lateral plate in that region.

My reason for dwelling at so great length on the derivatives of the peripheral layer of the protovertebra is, that this layer plays an important part in forming certain accessory portions of the pronephric system. I refer to the *capsule* of the pronephros. Already in the preceding stage I noted the occurrence of a lateral fold of the somatic layer immediately dorsal to the constriction between protovertebræ and lateral plates (Fig. 6). In the younger individuals of Stage IV. the fold covers the dorsal surface of the pronephric pouch, and extends a short distance down on its lateral surface (Figs. 18–21, *fnd. cps.*). In the older set of embryos it has reached the somatopleure ventral to the pronephros, and thus forms a complete investing capsule.

In frontal sections the fundament of the capsule may be seen to consist of a series of segmental outgrowths from the successive protovertebræ. Later, these segmentally arranged structures fuse into a continuous enveloping sheet.

Lateral to the pronephros the capsule presents in general a two-layered condition, the result of its having been formed as a fold; but on ascending to the level of the lower boundary of the somite, these two layers separate (Plate V. Fig. 45); one passes beneath the protovertebra, covering the pronephros on its dorsal aspect; the other is continuous with the somatic layer of the protovertebra, forming a lateral sheath to the myotome. These layers are present in the region both of the pronephros and of the duct, but are seen in their simplest condition in the region of the second nephrostome (Fig. 20); not merely because this is the middle of the pronephros, but also because the process is somewhat modified in the protovertebra next in front of it (somite II.). Somite II. is one of those in which a considerable portion of the kernel of the protovertebra is converted into mesenchyme. For this reason the inner layer of the capsular

fold, after separating from the layer which forms the lateral sheath of the myotome, passes inward, and is there lost in a loose mass of tissue (Fig. 18), resulting from the disassociation of certain cells of the somite in that region. Intersegmental regions also present appearances which are confused by the occurrence of cells belonging to the partition between two successive somites. The points which I especially wish to emphasize in this description are (1) the origin of the capsule from the somatic layer of segmented mesoderm, and (2) the fact that the layer from which the capsule is developed is also in other regions converted into mesenchymatic tissue.

In the younger specimens of this stage a horizontal fold of the splanchnopleure is to be noticed, forming a slight ridge directly across the body cavity from the pronephros. It first appears in front of the second nephrostome, and develops from this point backwards. It is the fundament of the glomus or pronephric glomerulus.[1] In the earliest trace of this organ that I have been able to find (Plate I. Fig. 8) there were already a few small mesenchymatic cells (*ms'chy.*) located in the angle of the fold. The source of these cells I have been unable to determine with certainty. The nuclei of all the cells in the fold itself lie very close to the body cavity, and it does not seem probable that those small cells could be produced by delamination from the splanchnopleure without an actual migration of the nuclei of the somatopleural cells to the basal, or entodermal, surface of that layer. I have never seen signs of such migration, and I therefore do not believe that it occurs. Furthermore, the folded portion of the somatopleure does not at once become thinner than the neighboring portions of that layer. In older stages, such a thinning takes place, but it seems to be due to a superficial extension of the layer, rather than to delamination. The position of the nuclei of the large entodermal cells in this neighborhood is equally unfavorable for the formation of these small cells by delamination. The only remaining explanation is that the latter have migrated into their present position from relatively remote parts. Other loose cells may be found between entoderm and splanchnopleure, and the question here raised is only a part of the larger problem as to the source of all such cells, including those which bound the yolk veins. The fate of the cells which I have found in the fundament of the glomus, I shall consider in treating of a later stage. I may, however, here anticipate to the extent of stating that they are connective-tissue elements.

[1] The former term seems to me preferable, and will be employed in the following pages. The exact relations of the glomus to the mesonephric glomeruli will be explained in the general discussion.

Figure 9 shows the fundament of the glomus in one of the older embryos of this stage. Within the hollow of the fold may be seen two cells (*ms'chy.*), which are to be regarded as the descendants of the first small cells to which I referred in the younger embryo. Their differentiation in the direction of connective tissue can be noticed throughout the whole extent of the fundament. The scattered rounded cells near them probably represent embryonic blood cells in the region of the aorta.

Stage V.

Plate I. Fig. 10. Plate IV. Figs. 31-34, 40.

The embryos belonging to this stage are on an average about thirty hours older than those of Stage IV. At this period almost all of the eggs are hatched; and, the duct having opened into the cloaca, the pronephros becomes functional. The larvæ of this stage measure 5–7 mm. in length, the rapid increase in size being largely due to the growth of the tail.

The form which the pronephros presents in this stage has been studied by means of reconstructions in the case of four pronephridia. The diagrams on Plate IV., Figures 31 to 38, represent in a rough way the number and distribution of the convolutions which the tubules present in this and the following stage. Of these, Figures 31 to 34 relate to the present stage. Figure 40 is a more accurate view of the pronephros which I have diagrammatically represented in Figure 32. In Figure 40 the outlines were taken with but little modification from the original reconstruction. I have not hesitated, however, even in this case, to remove defects plainly due to artificial causes, such as distorted sections and inaccurate superposition.

Comparing this drawing with Figure 39, it is easy to follow the changes that have taken place. In the earlier stage the fundaments of the three tubules are already present. The first modification which may be noted is the deepening of the constrictions which are indicated between the successive nephrostomes. In this way are formed three transverse tubules, joining distally a longitudinal canal; the former are the nephrostomal tubules, the latter I shall call the *collecting trunk*. In this case the continuation of the collecting trunk pursues a nearly straight course to the posterior margin of the gland, where it emerges as the segmental duct.[1] A second change which is apparent in Figure 40

[1] In Figure 40 the first nephrostomal tubule and the collecting trunk have a pink color, the second tubule is yellow, and the third is orange, whereas the segmental duct is uncolored.

is the growth of the collecting trunk in the region between the second and third nephrostomal tubules, and the consequent separation of the latter. The further complication in this case is mainly due to a convolution of the second tubule; slighter contortions occur in other parts. In the case of the pronephros diagrammatically represented in Figure 31, however, a canal, which corresponds to what we should regard in Figure 32 as the anterior portion of the segmental duct, has been folded first forwards, reaching nearly to the level of the first nephrostome, and then backwards. The bends which are convex anteriorly may be called the anterior bends; those which are convex posteriorly, the posterior bends. The universal occurrence of this condition in all older embryos makes it desirable to distinguish this bent portion of the tube and its derivatives both from the original longitudinal canal of the pronephros, which I have called the collecting trunk, and from the straight posterior portion, or segmental duct proper. In the following pages I shall speak of each *nephrostomal tubule* as extending from its origin in the nephrostome to its junction with the longitudinal canal, or collecting trunk. In the case of the first nephrostomal tubule, the point of union with the collecting trunk is usually marked by an abrupt change of direction; where this does not occur, however, the distinction between the two portions must be somewhat arbitrary. The *collecting trunk* forms the continuation of the first nephrostomal tubule, it receives in its backward course the second tubule, and may be regarded as terminating at the point of entrance of the third tubule. The *common trunk* arises from the point of junction of the third tubule with the collecting trunk, and, after making various convolutions, leaves the gland at its posterior end as the segmental duct. In the two pronephridia shown in Figures 31 and 33, we have before us examples respectively of the two principal forms of convolution which are to be recognized in subsequent stages, viz. the contortion of the second tubule and that of the common trunk. The third tubule finally undergoes convolution to some extent; but the first tubule and the collecting trunk take almost no part in the process. Although complication has appeared both in the second tubule and in the common trunk, it is to be noticed that these processes do not have a fixed sequence. I have numbered the diagrams on Plate IV. with reference to the state of development shown by the larvæ. In doing this, I have not been guided by the age alone, for the large amount of individual variation makes that method nearly valueless; but I have endeavored, by passing in review a large number of characters, to gain a notion of the relative degree of development shown by the larvæ.

The first of the series of diagrams (Fig. 31) shows complication to have taken place to a considerable extent in both the convoluted regions. In the next diagram (Fig. 32) the second tubule alone takes part in the complication. Figures 33 and 34 represent respectively the right and left pronephridia of one individual. In the right pronephros (Fig. 33) the typical condition of the common trunk is present, while the nephrostomal tubules have undergone no contortion. Likewise in the left pronephros (Fig. 34) it is the common trunk to which the increasing complication is due; but in this case there are two additional bends introduced by a slight folding backward of the middle of the anterior bend. The convolutions of the common trunk lie principally in the ventral portion of the gland. The tubes which in cross section are seen in the dorsal part are mainly the several nephrostomal tubules, and the collecting trunk. This condition is likewise retained in later stages.

The position of the pronephros with reference to the myotomes has not changed since the preceding stage. The whole structure is slightly longer, but the myotomes have also lengthened to the same extent. The three nephrostomes are situated, as before, beneath the first, second, and third myotomes posterior to the ganglion nodosum, and are segmental in position.

In all the embryos of this stage the duct has opened into the cloaca. It is to be remembered in this connection, that the morphological position of the duct is outside the somatopleure; so that the cœlom and two layers of mesoderm intervene between it and the intestine. As might be expected, the union does not take place until the segmented and unsegmented portions of the mesoderm have become separated from each other. The passage to the cloaca is then effected through the split thus produced, and consequently around the dorsal angle of the body cavity.

In the frog, there is a sharp histological contrast between ectoderm and entoderm, and there is therefore no difficulty in assigning a limit to the proctodæal invagination. The region into which the duct opens is the hind gut, and the intestine at this point is unquestionably lined with entodermal cells. The portion of the primitive gut posterior to the openings of the segmental duct forms the Amphibian cloaca, and corresponds precisely, I should say, with that part of the cloaca of Amniota which Gadow ('88, p. 28) has recently designated by the name *urodæum*. The wall of the intestine is not wholly passive in the union occurring between it and the duct. In front of the excretory openings, the lumen of the intestine has an elliptical form, its major axis being vertical.

On passing backwards, the dorsal half broadens and finally exhibits two lateral processes, or cornua, the walls of which are composed of a layer one cell deep. The ducts open into the distal ends of these cornua (see Fig. 27, showing the condition in Stage VI.). Behind the outlets of the segmental ducts, the lumen of the intestine has a nearly circular outline, and descends rapidly to the anus, or, as it may now more correctly be called, the cloacal aperture. I was able to see in Stage IV. faint traces of these intestinal cornua. The cells of the dorsal roof of the intestine showed in this region a looser structure, and a line of pigment indicated the region of the outfolding. The cells of the duct and those of the cloaca are histologically very different from each other, so that it is for a long time possible to draw a line sharply separating the two constituents where they have come in contact.

The pronephric system of tubules presents in this stage quite uniform histological characters. I shall therefore describe its typical condition, and then consider the modifications that are to be found in certain of its regions. The walls of the tubules are very thick, measuring on the average about 25 μ in thickness. They accommodate themselves readily to the structures with which they come in contact, becoming thinner opposite elevations in neighboring surfaces, and thicker next to sinuses. The size of the lumen varies greatly. In the segmental duct proper, the diameter of the lumen is about 25 μ; it is usually somewhat greater in the region of the convoluted tubules. The walls of the tubules are composed of an epithelium, consisting of a single layer of columnar cells. The radial dimension of the cells in the case of thick walls is approximately three times their width. Where the plane of the section cuts the wall of a tube tangentially, the cells may be seen to have a polygonal outline. The nuclei invariably occur close to the central lumen of the tube; each is large, and is usually provided with a single distinct nucleolus. The eccentric position of the nuclei is attended with a corresponding distribution of the cell protoplasm. By the picro-carmin method which I have employed, the yolk spherules take a bright yellow stain, and the nucleus a light red. The active protoplasm has a faint pink coloration, which, however, is wholly invisible if too much picric acid be left in the preparation. In young cells, where only a small amount of yolk has been consumed, the delicate tint of the protoplasm cannot be seen, since all the light passing through the section encounters yellow yolk spherules. As the consumption of the yolk progresses, the protoplasmic matrix comes into view. In the wall of the tubules, the yolk is crowded to the outer surface of the cell, and a sheet of protoplasm

first becomes visible close to the lumen. It is here also that pigment makes its appearance.

The histological character of special regions now claims our attention. The pronephridia shown in Figures 31 to 33 are all histologically very similar, but in the case of the gland represented in Figure 34 some notable differences occur, which I shall consider later. The somatopleure covering the pronephros is at this stage very thin. Each of the cells composing the membrane is thickest in its central portion, and tapers rapidly towards its margins. In the more advanced larvæ, the cells have elongated to such an extent that the peripheral portion is reduced to a thin protoplasmic plate, which is nearly devoid of yolk spherules. The central mass, on the other hand, contains the nucleus, and nearly all the yolk spherules. The peritoneum is continuous with the columnar epithelium of the walls of the tubules at the outer rim of the nephrostomes, which have the characteristic form of a funnel. Before reaching the periphery of the funnel, however, the columnar layer becomes slightly thinner, and at the rim it tapers rapidly, until it becomes continuous with the peritoneum (compare Fig. 18 of a younger and Fig. 28 of an older stage). The nephrostomal funnels are always deeply pigmented. The pigment is most abundant along the incurved surface, but is quite dense even up to the rim. It continues for a variable distance into the tubules. In the case of the pronephros, represented in Figure 31, the whole system of tubes was pigmented from the nephrostomes to the posterior bend near the beginning of the common trunk. The pigment granules are always disposed in a layer along the free surface of the cells. The nephrostomal tubules show in general the typical character, which I have previously described. The collecting trunk appears to be quite rigid, for I have never seen such a reduction of its lumen due to pressure as other tubes exhibit. The calibre of this canal is usually larger than that of the nephrostomal tubules. The portion of the duct which lies behind the third nephrostome is nearly straight and of uniform calibre. Generally the lumen is slightly wider, and the wall thinner, than in the nephrostomal tubules. In the pronephridia, shown in Figures 31 and 33, the loop embracing the anterior bend of the common trunk seems to have but little rigidity. It follows a tortuous course, and frequently the walls are so closely pressed together that the lumen is locally obliterated.

A peculiar modification in the pronephros, represented in Figure 34, has been alluded to. In this case, the common trunk, after proceeding from the level of the third nephrostome for a certain distance forward

along the ventral border of the gland, as in the other embryos, undergoes a change of structure at about the level of the second nephrostome. The lumen there begins to enlarge, and the wall to become thinner. Farther forward, the cavity of the tube becomes greatly dilated, and the bounding wall is reduced to a delicate pavement epithelium, having the same appearance as the peritoneum covering the pronephros. The tube again contracts shortly before attaining its most anterior bend. A similar dilation also occurs in the following stage, in the description of which I shall again refer to the chamber thus produced and suggest its possible function.

The pronephros at this stage is completely invested in a loosely fitting capsular membrane. The cells of which this envelope is composed have become very thin, so that they form a delicate sheet not more than 6 μ thick. The nuclei occur in slightly enlarged portions of the cells. They are rather small, and show a tendency to be flattened in the plane of the layer. At the lower outer angle of the myotome, the capsular membrane is continuous with the myotomal sheath, as in the earlier stage. The capsule covers the pronephros so loosely as to leave extensive spaces between the enveloping membrane and the tubules. These spaces, together with those between the convoluted tubes, form an extensive and complicated system of sinuses, which bound the pronephric tubules on every side (compare Fig. 28, belonging to the next older stage). Behind the last nephrostome, a considerable space intervenes between the wall of the capsule and that of the duct. There is thus formed a single continuous but irregular channel, which accompanies the duct throughout its entire course; it is also prolonged into the region of the gland as a large ventral sinus, which is triangular in cross section (compare the lower of the spaces marked *sn. sng.* in Fig. 28). This channel is the fundament of the posterior cardinal vein. The course of the vessel may be traced at this stage for a short distance behind the point where the ducts open into the cloaca. There are two veins connected with the anterior end of the pronephros. Of these the ventral one is the larger, and is continuous posteriorly with the cardinal vein. The dorsal vessel of the pronephros also unites with the cardinal vein by means of the spaces between the tubules. After passing forward and leaving the pronephros, the ventral vessel proceeds medianwards to empty into the sinus venosus, this vessel constituting the ductus Cuvieri. The dorsal vessel of the pronephros can be traced forward into the head. In the somite next in front of the first nephrostome, it lies between the ganglion nodosum and the myotome. It can be traced for some distance along the base of the

cranium, passing close to the median wall of the auditory vesicle and the ball of the eye.[1]

There are two kinds of cells found within the capsule of the pronephros concerning which I have as yet said nothing. Those which are more numerous are scattered, of circular outline and of unform size. Each has in general three or four large yolk spherules, and the nuclei are rather

[1] In order to ascertain, if possible, what vein of the adult this vessel represents, it will be necessary to describe here its condition in later stages. In the oldest embryos I have examined, 8.5 mm. long, the vein runs forward from the pronephros parallel to the aortic root and its continuation, the carotid artery. The vein is separated from the arterial trunk by the ganglia nodosum and faciale. Recalling the earlier position of the vein, it will be seen that it has been transferred from the median to the external side of the vagus nerve. In an intermediate stage, I have been able to see the nerve during its transit through the vein, thus confirming an observation of Kastschenko ('87, pp. 275, 276).

Following the vein farther forward, it is found to pass immediately ventral to the auditory vesicle, directly in front of which it sends a branch around the ganglion faciale to the side of the cranium. Slightly farther forward the vein divides, its branches passing around the more anterior of two ventral processes of the ganglion faciale. The two trunks thus formed separate. One enters the orbit, and can be traced to the anterior end of the optic bulb. The other passes below the eye, and pursues a nearly straight course to the anterior horn lip.

A description of the venous system of the adult frog has been given by Gruby ('42) and by Ecker ('64–81). The distribution of the veins which enter the dorsal portion of the pronephros corresponds most closely with the internal jugular of these authors. From the figures of Goette ('75), however, there can be no doubt that the vein I have described corresponds to the one which he calls the external jugular. I have been able to find a vein entering the sinus venosus directly which agrees accurately with the inferior jugular of Goette, but I have found none corresponding to the one he calls the internal jugular. It is stated by Goette (pp. 759, 760) that the vein named by him external jugular receives large branches from the maxillary and mandibular regions. This character would seem to connect it with the external jugular of Gruby and Ecker. According to Goette (p. 765), however, the external jugular of Gruby and Ecker is the same as his inferior jugular. I believe this statement to be true, and it seems possible that Goette, who confesses that his studies upon the veins did not extend beyond the first larval periods, may have erred in his account of the distribution of these rudimentary vessels.

Since the preceding description was written, a paper by Marshall and Bles ('90[b]) has appeared, which adds another to the divergent accounts I have reviewed. The inferior jugular of Marshall and Bles corresponds closely with the vein I have alluded to under that name. The anterior cardinal vein is described by these authors ('90[b], p. 236) as "formed by the union behind the ear of a jugular vein returning blood from the brain and dorsal part of the head, and a facial vein which lies superficially along the side of the head ventral to both eye and ear." These vessels are described in tadpoles, measuring 9 mm. in length. My own observations on larvæ of nearly this size do not agree with this description.

smaller than in the cells of the tubules. Very similar elements abound in the fundaments of blood-vessels at this stage, and it is evident that the cells are embryonic blood corpuscles. The spaces in which they occur constitute a complicated system of communicating blood sinuses, and are continuous with the lumens of the vessels entering and leaving the pronephros.

The other class of cells to which I have referred are mesenchymatic. I have carefully studied these cells in the endeavor to ascertain their precise origin. A mode of reasoning similar to that employed in discussing the probable origin of the inner cells of the glomus leads to the conclusion that the mesenchymatic cells of the pronephros cannot have been given off from the walls of the tubules. As I have stated, the cells in these walls are very thick, and their nuclei lie close to the lumen of the tube. Under these circumstances, it is difficult to understand how any cells of the tubule should divide so as to give off from their basal surfaces cells as small as those in question. The usual process of cell division, if it took place parallel to the surface of the layer, would result in the production of a small cell on the side toward the lumen and a large outer segment. Such a large cell might, it is true, by repeated divisions, break up into numerous small cells, but for several reasons I do not believe this to have been the case. If such a delamination and subsequent cell division took place, it would naturally be a conspicuous process; but I have never observed any evidences of it. This method of origin would involve a considerable thinning of the tubes, which does not take place.

There remain two other possible sources for the mesenchymatic cells of the pronephros. They may have arisen from the tissue bounding the pronephros, viz. the capsular membrane and the adjacent somatopleure, or they may have come from remote regions. In judging between these possibilities, it is important to consider the sudden appearance of the cells and the small amount of differentiation they have undergone. It seems to me highly improbable that they should have already accomplished any extensive migrations. Under these circumstances, such positive evidence as I am able to adduce is the more convincing. In studying the youngest stages in which mesenchyme was present in the pronephros, this tissue was usually found near the somatopleure or the capsule, and frequently consisted of a row of cells closely applied to one of these layers. Occasionally I have seen a layer of mesenchymatic cells arranged along the somatopleure in a very definite manner, so that the nuclei of the two layers lay directly opposite each

other and the intercellular regions precisely corresponded. In such cases the evidence seems strongly in favor of delamination, but I have never seen a nucleus dividing in that direction. This negative evidence, however, should have little weight, since all cell divisions occupy a comparatively short time, and are also obscured by the numerous yolk spherules. The observations just recorded agree very well with the rapid thinning of the somatopleure to which I alluded in discussing the histology of the tubules. I conclude, then, that the mesenchymatic tissue of the pronephros arises from the adjacent somatopleure, and probably also to some extent from the capsular membrane.

The glomus (Plate I. Fig. 10) has attained in this stage nearly its final dimensions. The lateral plate having become wholly detached from the protovertebræ, the glomus has the appearance of being attached to the wall of the body cavity at its dorsal angle (compare Fig. 9, of a younger stage, and Fig. 47, of Bufo). There is some individual variation, but in general it may be stated that the ridge constituting the organ under consideration extends continuously from the first nephrostome backward to a position slightly behind the third. It appears in cross section (Fig. 10) obovate, being attached by the narrower end. In structure it is very compact, so that it is difficult to locate with precision cell boundaries in the dense interior mass. The investing portion consists of a single layer of cells, which is continuous with the peritoneum. These cells are large, and have the form of spheres flattened on their inner surfaces (compare Plate VI. Figs. 49 and 50, *la. pi'ton.*, which represent this layer in Bufo). They are slightly pigmented, and a distinct row of pigment granules can usually be seen close to the inner surface of the layer. These outer cells are evidently the representatives of the large cells of the splanchnopleure which was folded, at a previous stage (see page 227), to form the earliest fundament of the glomus (Fig. 9, *fnd. glm.*). In certain favorable regions I have seen a thin structureless membrane lying directly within the outer cellular layer (compare Figs. 49, 50, *mb. ba.*). When any of the cells of that layer become detached, which frequently happens, this basement membrane usually remains in place, and gives a sharp outer contour to the glomus in that region. Besides the compact mass of large cells there occur within the organ one or two cells in each section (compare Figs. 49, 50, *en'th.*) which have an elongated form. They lie close to the basement membrane, with which their long axes are parallel. In sections each cell has a central swollen portion containing the nucleus, from which it tapers in both directions. I have not been able to trace the delicate lateral portions to their terminations, but I believe that

these cells form a complete endothelial lining, which follows closely the delicate basement membrane. They doubtless represent the loose cells alluded to in Stage IV. as occurring within the fundament of the glomus. Their origin I have already discussed in connection with that stage, where I showed that they were probably not derived from the outer layer of the glomus. Although the structure of the central mass of cells is, it must be admitted, somewhat obscure, I have found no evidences of the complication which Hoffmann ('86, p. 591) has recently maintained for it.

On the contrary, a comparison of many individual cells in this mass with the loose cells in the cavity of the aorta has made me confident that most of the cells contained in the glomus are embryonic blood corpuscles. It is possible, however, that others are derived from infolded portions of the outer layer of the glomus. They appear to have no representatives in early stages of the organ. In my opinion, then, the glomus is essentially a blood sinus, the wall of which projects into the body cavity, carrying before it the peritoneal layer.

The junction of the two aortic roots takes place very nearly opposite the first nephrostome (compare Plate IV. Fig. 28, *rx. ao.*). The aortic trunk thus formed (Fig. 10, *ao.*), since it occupies the space between the chorda and mesentery, passes close to the attachment of each glomus.

The precise relations of the aorta to the glomus are rather difficult to observe, since the former is peculiarly liable to injury in sectioning. The interior of the chorda at this stage consists of a frail vesicular tissue, whereas its outer sheath is tough, and resistant to cutting instruments. In sectioning, therefore, it collapses, and occasions serious distortion of the adjacent parts.

In the younger individuals of this stage, the cavity of the aorta did not seem to be sharply marked off from the root of the glomus; in several instances, indeed, I was able to observe a continuity between the endothelium of the aorta and that lining the glomus. In older individuals I have repeatedly noticed distinct branches from the aorta passing into the glomus (Plate I. Fig. 10, *va. sng.*). These observations were made, however, only on the most favorable sections, and I have been unable to ascertain the number or distribution of such branches. In both of the two most obvious cases, however, the vessel entered the hinder end of the glomus. Occasionally, the vessel to the glomus seems to be only a lateral branch given off from a vessel which can be traced between entoderm and splanchnopleure for some distance ventral to the glomus (Fig. 10, *va. sng.*, the lower of the two dotted lines).

I have spoken of the expanded dorsal portion of the body cavity, into which the nephrostomes open, and which contains the glomus. This portion of the body cavity constitutes the so-called pronephric chamber. It is not to be regarded as a closed cavity. Elsewhere the somatopleure and the splanchnopleure are closely applied to each other, but there is absolutely no fusion of these layers ventral to the pronephros.

Stage VI.

Plate III. Fig. 27. Plate IV. Figs. 28, 30, 35-38, 41. Plate VI. Fig. 51.

The larvæ included in this stage are in general two or three days older than those of the preceding stage. They are about 8 mm. long from the anterior end to the tip of the tail. In this stage, the body no longer tapers gradually from the branchial region to the posterior end; but a definite line of separation is established between the trunk and tail regions. In the tail a distinct membranous fin has appeared, both along the dorsal and the ventral median lines. The horn lips can be seen surrounding the mouth, and the external gills project prominently on both sides of the body.

The pronephros of this stage has developed along lines foreshadowed in the preceding stage. The general form of the organ can best be understood by reference to the series of diagrams (Figs. 35–37) and the reconstruction (Fig. 41) given on Plate IV. As will be evident at once, the gland has reached a high degree of complexity, produced, however, by a continuation of the same process of complication which had begun in Stage V. Thus the first nephrostomal tubule[1] and the collecting trunk retain throughout a nearly unmodified condition; the third nephrostomal tubule usually becomes slightly complicated; the second exhibits the greatest number of convolutions. The common trunk, however, is the part which has been principally concerned in producing the increased complexity of the gland. It is to be noted that this contortion is not of a wholly indefinite nature; indeed, there is considerable uniformity in the pronephridia of different individuals of the same stage of development. In Figure 31, representing a pronephros of a larva in Stage V., it is to be seen that there are only two bends in the common trunk, which extends forward to the anterior end of the gland. From this simple condition the later complications may be derived by a few simple steps. In order to follow the changes it will be advisable to

[1] The same colors have been employed for corresponding parts in both Figures 40 and 41. Consult explanation of Figure 41.

distinguish: (1) posterior bend adjacent to the collecting trunk, (2) ascending arm, (3) anterior bend, and (4) the descending arm, which is continuous with the segmental duct. The simplest condition which I have found in Stage VI. is represented in Figure 35. This diagram relates to a larva of R. sylvatica Le C., and it is of interest to note its close similarity to Figure 38, which represents the pronephros of a larva of R. pipiens Schreb. (halecina) of this stage. These two pronephridia will be considered together. In both, the ascending arm of the common trunk makes either an S-shaped bend or a loop interpolated near the middle of its course; the transverse portion, or anterior bend, is thrown into one or two slight folds, and the descending arm shows two loops, one in the middle of the gland, and the other near its posterior end. The two remaining diagrams (Figs. 36, 37), though taken from different individuals, are alike in all essential particulars. The principal changes from the condition shown in the simpler pronephridia just described consist in the development of an additional loop in the course of the ascending limb, and of several slight folds in the transverse portion; the loops present in the younger individuals of this stage have persisted and become more extensive. In the case of the larva whose pronephros is represented in Figure 37, I made a comparative study of the pronephridia found on the two sides of the body. The comparison showed that a slight want of symmetry existed between the two sides. Occasionally the direction in which equivalent tubes were bent did not correspond. On the right side of the body (the one figured), for example, the hindermost loop of the descending arm was formed by an inward bend, while in the left pronephros the corresponding tube is bent outward. In the descending arm of the left pronephros a small loop occurs in addition to those present on the right, while one of the two loops occurring in the ascending portion of the right side is almost unrepresented on the left; thus, the right pronephros approximates in this respect the simpler organ represented in Figure 35. A more striking anomaly of the left pronephros consists in the occurrence of a slight bend of the collecting trunk between the junctions of the second and third nephrostomal tubules, so that the latter connects with an ascending portion of the collecting trunk. Finally, the third nephrostomal tubule of the left side joins the collecting trunk farther posteriorly than does the one on the right side. In general, however, it seems to me that the several pronephridia studied show a rather remarkable uniformity even in the details of the arrangement of their tubules.

The position of the pronephros with reference to the muscle plates is

the same in this stage as in the foregoing. The lateral plate is now wholly cut off from the myotomes; but a study of serial sections shows that each nephrostome lies beneath a myotome. These myotomes correspond to somites II., III., and IV.

The course of the duct in this stage is the same as in Stage V. The openings into the cloaca (Plate III. Fig. 27, *dt. sg.*) are now situated at the bottom of a depression in the dorsal wall of the cloaca (*clc.*). While the excretory products enter the main cloacal chamber by a single aperture, a glance at the histological characters of the short median unpaired trunk shows that it is lined with entodermal cells, and is therefore really a diverticulum of the roof of the cloaca. The ducts of the two sides, therefore, are not to be regarded as uniting into a common trunk, but as opening separately into a dorsal diverticulum of the cloaca.

The histological characters of the pronephric system have not undergone any great changes since the preceding stage. Figure 28 (Plate IV.) shows a cross section of the left pronephros of the larva, whose right pronephros is diagrammatically represented in Figure 37. The plane of the section passes through the first nephrostome, and the transition from the pavement cells of the peritoneum to the columnar epithelium of the tubules is clearly shown. This section also shows, besides the first nephrostomal tubule, the anterior ends of two loops which belong to the transverse portion of the common trunk. The walls of all the tubules are thinner than in the preceding stage, and since the nuclei remain of about the same size as heretofore, they now occupy a far larger proportion of the cell, and in the case of the thinnest-walled tubules are frequently almost in contact with both the outer and inner surfaces of the cell. The amount of yolk in the cells is considerably lessened, especially in those parts which exhibit the greatest number of convolutions. In some cells, a single large spherule is the sole remnant of the formerly abundant yolk. Pigment is present as scattered grains in the walls of all the tubules; it also shows a tendency, as in the previous stage, to accumulate along the free surfaces of the cells. The nephrostomes, however, are densely pigmented on the surface that is directed towards the body cavity and the lumen of the tubule. The duct posterior to the pronephros (Fig. 30) offers no features worthy of special mention. It is accompanied throughout by the cardinal vein (*vn. crd.*), on the median side of which the earliest fundaments of the mesonephric tubules are visible.

I have described a special enlarged region of the convoluted duct in a larva of Stage V. A similar condition is apparent on both sides of the

body in the case of the individual whose pronephros is represented in Figure 35. The dilated chamber (Plate VI. Fig. 51) is here formed by a great expansion of that portion of the ascending arm of the common trunk (*trn. com.*) which is adjacent to the collecting trunk (*trn. clg.*). A similar dilated chamber occurs in the pronephros represented in Figures 36 and 41; but in the latter case neither the dilation of the lumen nor the thinning of the wall is very pronounced. In both these cases the expanded chamber is present in portions of the tubular system which are exactly equivalent to each other. Under these circumstances, the expansion of the *descending* limb of the duct occurring in the pronephros of Stage V. (Fig. 34) seems quite anomalous. The dilated chamber is invariably, however, superficial in position, lying close to the capsular membrane. I have been unable to reach an entirely satisfactory opinion regarding its function. Since it is situated so near to the nephrostomes, it does not seem very well adapted to serve as a reservoir for the storage of fluids secreted by the gland, for by far the larger portion of the secreting surface is situated between it and the duct. However, the chamber doubtless receives whatever fluids are gathered by the nephrostomes or are secreted by the peritoneal tubules, and it is possible that the enlargement exists solely for this purpose. In following the duct from the dilated region towards its outlet, a greatly contracted portion is reached, and this may serve for the better retention of fluid contained in the chamber.

The capsule in these larvæ is not so well marked as in those of the preceding stage. Between the pronephric tubules and the ectoderm there has arisen a considerable quantity of mesenchyme, and the capsule now appears merely as the line along which this mesenchyme comes in contact with the pronephric tubes and blood sinuses.

In discussing the blood supply for the preceding stage, it seemed advisable to consider the vessels in older larvæ as well, and I shall therefore merely refer here to the account given in that connection.[1]

[1] In all the larvæ of this stage which I have examined, I have observed a peculiar sac, of which I have been unable to find any mention in the literature. In the oldest larva of this stage it consists of a capacious sinus lying in the triangular area bounded by the myotomes, the somatic peritoneum, and the ectoderm. It extends backwards from the niveau of the third nephrostome for a length of two or three myotomes, and appears to be closed upon all sides. The sac lies in a mass of loose mesenchyme, but possesses firm walls, so that any opening would naturally be easily recognizable. In the interior of the sac, cells which are undistinguishable from blood corpuscles are found in considerable numbers. In a younger larva the sac occurs in a corresponding position, is nearly filled with blood cells, and is in open

The glomus is somewhat larger and more compact than in the preceding stage, and for that reason its structure is more obscure; but I have seen nothing which would lead me to believe that it differs materially from the condition exhibited by the younger glomi of Stage V. The organ is bounded by a definite peritoneal layer and contains blood cells together with embryonic connective-tissue stroma. The blood cells are usually contained in definite channels, and, being closely packed together, frequently appear in cross sections to be disposed with considerable regularity around a central point. This arrangement is naturally suggestive of a tubular or a rod-like structure; but the histological characters of the cells and the conditions exhibited by adjacent sections show that this impression is illusory. In short, I have been unable to find within the glomus any traces of the rods and thick-walled tubes which have been described by Hoffmann ('86, p. 591).

No closed pronephric chamber exists at this stage. In the most anterior sections in which the pronephric tubules appear, a blind anterior diverticulum of the body cavity is to be seen; but this unites with the general body cavity surrounding the intestine even before the niveau of the first nephrostome is passed. Throughout the remainder of the pronephric region the lung bud (Plate IV. Fig. 28, *lnd. pul.*) forms a ridge on the splanchnic side of the cœlom. This ridge partially separates the pronephric chamber from the general body cavity; and in the region of the third nephrostome a still more perfect closure is effected on the right side of the body by means of the approximation of a portion of the midgut to the peritoneum covering the pronephros.

Stage VII.

The age of the larvæ of this stage, reckoned from the time of fertilization, is about forty-seven days. A large gap therefore intervenes between Stages VI. and VII., and the older larvæ are studied merely for the purpose of observing the process of degeneration in the pronephros. In the larvæ of Stage VII. the mesonephros has already attained a degree of complication comparable to that gained by the pronephros at Stage VI., i. e. the same average number of tubes appear in cross sections through the two glands. The mass of contorted tubules in the case of the mesonephros, however, is formed wholly by the transverse tubules, while the

communication with the cardinal vein. In a larva of intermediate age, the sinus communicates with the cardinal vein by means of a very narrow canal. Respecting the fate and the significance of this singular structure, I have no suggestions to offer.

duct pursues a direct course through the gland. The duct is situated in the dorsal portion of the mesonephros adjacent to the lower borders of the myotomes; its relations are therefore different from those of the longitudinal canal of the pronephros, since, as we have seen, the common trunk in the pronephros is greatly convoluted, and its windings occupy the ventral portions of the gland.

The marked signs of degeneration which the pronephros presents in this stage prevented my reconstructing the gland, since it proved to be impossible to follow any given tube throughout the entire series of sections. Indeed, I am convinced that the tubules are no longer strictly continuous. I must therefore content myself with a brief description of the histological features noticed.

The lumen of the tubules is greatly enlarged, and is frequently filled with a dense coagulum which stains similarly to protoplasm. The cell walls are very thin and show a tendency to become shredded or frayed along the interior surface. The membranes between the cells in the wall have become indistinct, and the number of nuclei in a given area is far less than in a corresponding portion of the wall in Stage VI. The nuclei are stained only feebly, but contain deeply staining granules, and seem to be disappearing, since one can observe numerous gradations between the typical nuclei and those which have become so pale as to be nearly invisible. The ground substance of the walls is slightly vacuolated and contains numerous scattered dark granules. Between this remnant of the cellular wall of the tube and the basement membrane, I have frequently seen small cells with deeply stained nuclei. These may possibly represent intrusive connective-tissue elements.

I regret that I have not been able to make an extended study of the degeneration of the pronephros; but the limit which I have set to my work is perhaps the least arbitrary which I could easily make.

B. Bufo.

The development of the pronephros and the segmental duct in Bufo is very similar to that which I have described for Rana. For this reason, I can treat the development in Bufo much more briefly, and shall lay principal stress upon those features which are unlike in the two genera.

Stage I.

In the case of Rana, this stage included embryos which showed an ill defined somatopleural thickening lying immediately posterior to the cranial ganglionic mass. This proliferation proved, on comparison with

older specimens, to be the first indication of the pronephric thickening. A similar condition of the somatopleure is presented by embryos of Bufo about 2 mm. long, in which the medullary folds are widely open.

The general relations of the germinal layers at this stage are almost identical with those in Rana, and the same histological criteria for distinguishing them can be employed. The ectoderm is very sharply marked off from the mesoderm. The former is deeply pigmented, while the adjacent mesoderm is almost destitute of pigment. The yolk spherules of the ectoderm measure on the average about 2 μ; those of the mesoderm, about 4 μ.

In embryos in which the medullary tube is still widely open, the somatopleure and splanchnopleure are separated from each other by a distinct space, the cœlom, which can be traced with perfect distinctness into the protovertebral plate, where it becomes slightly expanded. In the anterior half of the embryo, both the somatic and the splanchnic layers are only one cell in thickness. Posteriorly, and in the middle trunk region, however, certain loose cells bordering on the cœlom become associated with the somatic layer; but this layer is never, except at the extreme hinder end, more than two cells in thickness.

Stage II.

Embryos in which the medullary tube is just closed exhibit a condition of the mesoderm slightly different from that of Stage I. In the posterior portion of the embryo, the mesoderm is quite thick in the region of the protovertebral plate, and becomes gradually thinner as it approaches the ventral portion of the body.

Anteriorly, the protovertebral plate shows traces of the differentiation of four or five protovertebræ. Of these, the most anterior lies in the same transverse plane as the ganglion nodosum, and, following the method of designation which was employed in the case of Rana, would properly represent somite I. This protovertebra, as in Rana, shows signs of transformation into mesenchyme, and is considerably compressed in the region of the ganglion.

The thickening has the general form which I have described for the corresponding stage of Rana, and its anterior margin is situated under somite II.

In the region of its greatest thickness, which is somewhat lateral to the boundary between the protovertebra and the lateral plate, it is two or three cells deep. It thins out slowly on the ventral side, much more rapidly on the side of the protovertebra, or dorsally. The thickening

involves the ventral portion of the lateral wall of the protovertebra itself, although the greater part of the thickening is in the region of the lateral plate. I have not been able to find any sharp plane of division marking the lower limit of the thickening. The latter extends posteriorly through a distance of three or four somites, but it is difficult to make out its relations to the protovertebræ, in consequence of the small amount of differentiation which these exhibit at this stage. It seems to me, however, that the thickening reaches backward into a region posterior to that in which the pronephric tubules later develop, and therefore represents already the first fundament of both the pronephros and the anterior end of the segmental duct.

Frontal sections show the same relations between the pronephric thickening and the protovertebræ that I have described for Rana, but in Bufo the cœlom is entirely obliterated by the growth of the pronephric thickening, and consequently the pronephric chamber described in a corresponding stage of Rana does not exist in Bufo. This circumstance renders the determination of the precise boundaries between the two layers of mesoderm somewhat more difficult in the Toad than in the Frog, but still there is usually an unmistakable line of division between somatopleure and splanchnopleure even in the former. The pronephric thickening at this stage is from two to three cells thick, and is a solid mass.

Stage III.

In embryos of this stage, the fundament of a single pair of gill-folds is present; the fundament of the auditory vesicle consists of a simple thickening, which is just beginning to separate from the superficial ectoderm; and five or six protovertebræ have made their appearance. The embryos measure from 2.25 to 2.50 mm. in length.

The pronephric thickening becomes sharply marked off in this stage from the undifferentiated mesoderm lying ventral to it, and the canalization of the structure is accomplished by the arrangement of the cells around a lumen. Segmentally, the pronephric thickening has in general the form of a close fold of somatopleure, whereas intersegmentally it appears as a flattened tube. The points of continuity with the cœlom are situated each directly beneath the middle of a protovertebra, and the somites in which they appear are II., III., and IV.

The duct arises as a backward continuation of the pronephric thickening, and contrasts very sharply in histological characters with the ectoderm, in consequence of the pigmentation and paucity of yolk spherules in the latter.

Stage IV.

Plate V. Fig. 43.

Embryos of this stage measure from 2.8 to 3.1 mm. in total length. Muscular fibres have begun to appear in the myotomes, the auditory vesicles are entirely detached from the external ectoderm, and the protovertebræ have been differentiated as far back as the anus.

The pronephric pouch of Bufo is very similar to that of Rana. It communicates with the cœlom by means of three nephrostomes, and from its ventral margin the duct takes its origin. The nephrostomes are segmental in position, and are situated beneath protovertebræ II., III., and IV.[1]

The duct can be followed for some distance posterior to the hindermost pronephric nephrostome as a distinct elliptical tube with a central lumen. The lumen, however, disappears further posteriorly, and the duct terminates either as a simple thickening of the somatopleure, or its posterior end merely rests upon the mesoderm in the region of somite XI. The hinder tip of the duct (Fig. 43, *fnd. dt. sg.*) in both cases resembles very closely the adjacent mesoderm both in the size and in the abundance of yolk spherules, and it differs from the ectoderm both in these features and in the scarcity of pigment. In Bufo I have never been so fortunate as to find the growing end of the duct situated in a groove of depressed mesoderm; but I believe that the fundament extends itself from the region of its origin in the somatopleure to the projecting cornu of the cloaca by means of an independent growth on the part of its own cells. The greater part of the duct, however, arises from a local proliferation of somatopleure.

The pronephric capsule in Bufo arises as a downgrowth from the outer peripheral layer of the protovertebræ. In this stage, however, it has not reached the somatopleure ventral to the pronephros, but merely forms a two-layered scale-like sheet of tissue covering the dorsal portion of the gland.

The pronephric chamber is present at this stage. The general body cavity, however, has not yet appeared, the somatopleure and splanchnopleure being in other regions in close contact.

[1] I have preserved in the enumeration of the body somites of Bufo the same designations that were employed in the case of Rana. In Bufo, however, the kernel of the degenerate protovertebra in front of somite I. gives rise to a few muscle fibres

Stage V.

Plate V. Figs. 42, 46. Plate VI. Figs. 47, 49, 52.

At this stage the larvæ were hatched and swam about freely in the aquaria. The larvæ measured from 4 to 6 mm. in length, and each had a distinct tail, which protruded for a distance of 1.5 to 2 mm. behind the anus. The pronephros was probably already functional.

The character of the convolutions of the pronephric tubules was studied in the case of four pronephridia. In this feature one of them corresponded very closely with the condition in the pronephros of Rana represented in Figure 33. The remaining pronephridia differed from this type solely in the circumstance that the third nephrostomal tubule joined the collecting trunk at the extreme posterior portion of the bend, which in Rana usually forms the first portion of the common trunk.

The position of the pronephros with reference to the somites remains in general nearly the same as in the preceding stage. In individual cases, however, the nephrostomes do not appear to lie precisely under the middle of the myotome.

In embryos of this stage, the segmental ducts already open into the cloaca. These openings are situated beneath myotome XII. It is obvious from this fact that the duct in the older embryos of Stage IV. had already very nearly reached the region of its final communication with the cloaca. In Bufo the lumen of the gut is very narrow, and is separated from the lateral walls of the body by an extensive mass of yolk cells. The cloacal cornua are therefore in this case very long, extending to the outer surface of the entoderm. The ducts reach these cornua by passing between the dorsal angle of the body cavity and the overlying myotomes.

The histology of the pronephros in Bufo does not present any noteworthy features of difference from that in Rana. The tubes are all slightly smaller in Bufo, and their walls contain somewhat more pigment than do those of Rana.

The capsule envelops the pronephros and duct in the way that I have described for Rana, and it also encloses a series of blood sinuses which are developed from the posterior cardinal vein. I was not able to obtain in Bufo any additional evidence in regard to the origin of the mesenchyme of the pronephros.

Two veins emerge from the anterior end of the pronephros. One of these is the immediate continuation of the posterior cardinal vein, which, in passing forward as the ductus Cuvieri (Plate V. Fig. 42, *dt. Cuv.*), makes a rapid ventral descent to open into the sinus venosus. The

other vein (Fig. 42, *vn. jgl.*) passes forward between the myotome and the vagus nerve. It evidently is one of the jugular veins, but I have not been able to study its distribution in later stages, and am therefore unable to state more precisely which vein of the adult it represents.

The structure of the glomus in Bufo is far more evident than in corresponding stages of Rana. In treating of the development of the glomus in the latter, I reached the conclusion that it arises as a simple fold of splanchnopleure, into which mesenchymatic cells migrate. In later stages I was able to identify the original outer sheath with a distinct basement membrane, and found within this membrane a large number of embryonic blood corpuscles, and occasionally certain cells which resembled in their histological characters those of the sheath or peritoneal layer. In Bufo the vascular system is less developed than in the corresponding stage of Rana; and, owing to the small number of the blood corpuscles, the remaining cellular elements come more plainly into view. The usual form of the glomus is that of a hollow peritoneal sac lined with endothelium (Plate VI. Figs. 47, 49, 50), and containing scattered blood corpuscles (Fig. 46). At the entrance to the sac the endothelium (*en'th.*) is continuous with the loose mesenchyme surrounding the aorta, and, in certain regions, the lumen of the latter can be traced into the interior of the glomus. This organ, then, exhibits markedly the character of a blood sinus, the walls of which project into the body cavity. Occasionally one encounters in Bufo certain minor pocketings of the peritoneal layer of the glomus, — invaginations into the lumen of the glomus at the place, e. g., occupied by the letters *cœl.''* (Fig. 52). If the cells at the apices of such invaginations were to become detached, this condition would serve to indicate the source of the pigmented cells found in the interior of the glomus in the case of Rana, although I have as yet reached no final conclusion in regard to this matter.

In this stage the body cavity exists as a distinct lumen only in the region from which the nephrostomes emerge, where it constitutes a pronephric chamber.

My studies on the development of the excretory organs in Bufo have not extended beyond the present stage.

C. Amblystoma.

Plate V. Fig. 44. Plate VI. Fig. 48. Plate VII. Figs. 53-56. Plate VIII. Figs. 57-65.

Amblystoma shows in the development of its excretory system many features of similarity to the Anuran forms already described. The dif-

ferences, however, are far greater than those which exist between Rana and Bufo, and will require for their presentation a fuller treatment than was given in the case of the latter genus; but the development in all three genera is sufficiently similar to allow the recognition of the same successive stages, based upon the degree of complication exhibited by the pronephros.

Stage I.

Plate VI. Fig. 48.

In embryos of this stage, the two lateral medullary folds have just fused to form the neural tube. The embryos have a slightly elongated form and measure about 3.7 mm. in length. They are slightly more advanced than the embryo of Amblystoma represented by Bambeke ('80, Planche XI. Fig. 35). The eggs from which I derived my series of embryos had been deposited for a variable length of time before they were collected, and I am unable to give the ages of the several stages.[1]

The general arrangement of the germ layers (Plate VI. Fig. 48) is similar to that which I have described for Rana and Bufo. The ectoderm (*ec'drm.*) consists in general of a single layer of cells, each of which has the form of a cube slightly flattened. Scattered ectodermal cells form an incomplete deep layer, which may gain in some regions, e. g. in the head, a very considerable development. The outer face of each ectodermal cell possesses a thin layer of pigment, but this is by no means so dense as in Rana and Bufo. At this stage yolk spherules are abundant in all the cells of the ectoderm.

The entoderm has nearly the same arrangement as in Rana, but the yolk cells are relatively more abundant, and the lumen of the gut is narrower. In the anterior region, the chorda consists of a simple fold in the dorsal roof of the intestine; but in the posterior portion of the body it is represented by a single row of high columnar cells, which form a layer convex from side to side towards the lumen of the intestine. This layer is the one which O. Hertwig ('83) has named the chorda-entoblast. The cells of the yolk entoderm are in general the largest in the

[1] A quantity of the eggs of Amblystoma punctatum Linn. raised in the laboratory during the present season reached the several stages as follows: Stage I., 5 days; Stage II., 5 days, 12 hours; Stage III., 6 days, 15 hours; Stage IV., 7 days, 15 hours; Stage V., 8–14 days; Stage VI., 15–20 days. These figures are only approximate, and between Stages II. and V. the individual variation is frequently more than sufficient to cover the entire interval between two successive stages. The temperature of the water varied somewhat during the period, but I believe that 10 or 11° C. would be a fair average.

body, and contain very large yolk spherules. The majority of the entodermal cells contain no conspicuous accumulations of pigment; but the latter may occasionally be found in considerable quantity, particularly in the cells bordering on the gut.

In the dorsal portion of the body, the mesoderm consists of two lateral masses of tissue, each of which spreads outward and ventralward from the neural tube, and joins its fellow of the opposite side in the ventral median line. Each of these masses of mesoderm is thickest next to the medullary tube, and gradually becomes thinner in passing outward around the mass of yolk cells. In the dorsal half of the body (Fig. 48) each mass of cells consists of two distinct layers, which are continuous with each other along the sides of the neural tube. They represent the first division into somatic (*la. so.*) and splanchnic (*la. spl.*) mesoderm, and the slight space which separates them is the cœlom (*cœl.*). On passing outward and ventrally, the two layers of mesoderm gradually approach, and at length are continuous with, each other; for a short distance farther, it is still possible to trace two rows of nuclei, indicating approximately the territory occupied by the layers; but this arrangement finally disappears, and before the ventral surface is reached the mesoderm has the form of a layer only one cell in thickness (*ms'drm.*).

In both somatic and splanchnic layers, the cells are of a nearly cubical form, but those of the parietal layer are rather thicker, and may be even columnar. The mesoderm of the ventral side of the body, on the other hand, is composed of more flattened elements. The cells of the mesoderm are in general intermediate in size between those of the ectoderm and of the entoderm. Their yolk spherules are much smaller than those in the entoderm, but resemble those in the ectoderm too closely to afford a thoroughly satisfactory criterion for distinguishing the two layers. The mesodermal yolk spherules are, however, *slightly* larger than those of the ectoderm; and in doubtful cases they may be taken into account.

The pigment of the mesoderm is usually collected along that surface of the cell which faces the cœlom, and may in part serve as a guide for following that cavity in cases where the bounding layers of mesoderm are in close contact with each other.

I have spoken of the somatic mesoderm as a layer a single cell in thickness; this is not, however, an adequate representation of the actual condition. In many sections there may be observed, from place to place, an additional cell associated with the otherwise single layer. The occurrence of an incomplete second layer of cells is most noticeable in the anterior portion of the trunk, in a region directly lateral to the protover-

tebral plate. It is probable that this slightly thickened somatic layer is the first indication of the pronephric thickening.

Stage II.

Plate V. Fig. 44.

Embryos of this stage measure nearly 4 mm. in length; the medullary tube has become entirely separated from the superficial ectoderm, and three protovertebræ can be distinguished in longitudinal sections.

The fundament of the pronephros forms in this stage (Plate V. Fig. 44) an evident thickening of the somatic mesoderm lying immediately lateral to the protovertebral plate. Throughout the greater part of the thickening, the layer is obviously two cells thick, and occasionally three nuclei may be seen in a line perpendicular to its surface. The cells constituting the thickening are closely compacted, and do not appear to form definite layers. The fact that the thickening passes through a stage in which it is only two cells in thickness precludes the possibility of its being a disguised fold with closely applied walls, for in that event there must be at least three layers of cells involved. Neither the anterior nor the posterior limit of the thickening can be clearly determined at this stage. I am also unable to state definitely its relations to the protovertebræ, inasmuch as these cannot be adequately made out in transverse sections, and the extent of the thickening cannot be satisfactorily observed in such longitudinal sections as pass through both the protovertebræ and the pronephric thickening. The latter may be traced for a distance of about 0.5 or 0.6 mm. Each protovertebra at this stage measures about 0.27 mm. in length, so that the thickening extends through a length of about two protovertebræ.

In slightly older embryos the pronephric thickening becomes in general three cells in thickness; but it is still a solid proliferation, with no indication of extensions of the cœlom between the layers.

Stage III.

Plate VII. Figs. 55, 56.

At this stage the young Amblystomas are about 4.3 mm. long and distinctly elongated in shape; but they show as yet no trace of a tail. They are further characterized by the possession of about eight well marked protovertebræ.

In all the embryos of this stage the pronephric thickening is at least three cells in depth, and has a definite ventral boundary. The thickening extends as far forward as the front face of somite III., and posteriorly

tapers gradually into undifferentiated somatopleure. The backward prolongation of the thickening is the first fundament of the segmental duct, and may be traced at least as far back as somite VI. Both portions of the thickening appear to arise in the same way; namely, by cell proliferation in the somatopleure.

It is a matter of some difficulty to ascertain when the first trace of a lumen appears. Before the two walls actually separate, the nuclei frequently show an arrangement which is suggestive of an evagination; but one cannot always trust such appearances. Later, a line of pigment can be traced from the body cavity for some distance into the interior of the thickening, and finally the two walls separate, leaving a clearly defined lumen. In all cases, the two regions of continuity with the cœlom are opposite the middle of protovertebræ III. and IV. respectively; and there is no indication whatever of a continuous fold.

Although the pronephric mass thus shows evident signs of segmentation, yet, as is to be seen by a comparison of segmental and intersegmental regions (Plate VII. Figs. 55 and 56), the proliferation is not interrupted in the latter regions. In frontal sections through pronephridia in which a definite lumen has begun to appear (compare Plate VII. Fig. 55), there can be seen two narrow canals leading from the cavities of protovertebræ III. and IV. and extending outward as cœlomic diverticula into the pronephric mass. From this condition the hasty conclusion might be drawn that the narrow canals are in fact outgrowths from the *protovertebral* cavities. This however, in my opinion, is not the case. If the relations of the mesoderm in such a transverse section as is shown in Figure 55 be regarded, it will be seen that a frontal section through the pronephric region (in the figure cited, a horizontal section a little below the level of the letters *cœl.'*) would cut through the protovertebral cavity near its floor, and at the same time pass through the lumen of the pronephric thickening. Since, moreover, these two spaces are continuous by means of the communicating canal, it might at first appear that the latter belonged to the pronephric tubule. The fate of that portion of the tube, however, shows this interpretation to be incorrect, and that it was only by means of the communicating canal that the lumen of the pronephros communicated with the protovertebral cavity; for when the separation of the protovertebræ from the lateral plate takes place, the communicating canal, which is assumed to be the stalk of the pronephric diverticulum of the protovertebra, becomes closed, and the pronephros is thereby left in communication with the body cavity alone (compare Mollier, '90, Taf. XII. Figs. 10 *c.*, 10 *d.*, tr_1 and tr_2).

Stage IV.

Larvæ of Amblystoma do not possess a conspicuous widely open pronephric pouch, such as has been described in Anuran species; but the proliferation becomes at once converted into a tubular organ. Indeed, the condition of the pronephric thickening in Stage III. is the one which is most similar to the Anuran pronephric pouch, since it is then a continuous structure having connections with the cœlom in segmental regions.

In slightly older embryos, the dorsal half of the pronephric thickening is no longer continuous through the region between protovertebræ III. and IV.; and from this region backward to the hinder face of protovertebra IV. the mass is distinctly divided into two tubes. Of these two tubes, the more median and dorsal is the second nephrostomal tubule; the more lateral and ventral is the common trunk. Finally, it is to be observed in a number of cases that an anterior loop of the common trunk occurs a short distance in front of the point of junction with the nephrostomal canals. The pronephros thus has a form which approximates very closely to the condition which forms the starting point for the next stage (Plate VIII. Fig. 58).

Stage V.

Plate VIII. Figs. 57-60.

This stage includes embryos which have attained a length of from 5 to 6 mm. Many of the older embryos of the stage have already hatched; they possess well developed tails and swim about freely.

The general form of the pronephros has been studied by means of a number of rough reconstructions, some of which are represented by the diagrams on Plate VIII. In Figures 57 to 60 inclusive, which belong to this stage, no windings have been reproduced which were not of sufficient magnitude to form definite antero-posterior loops; and, further, in plotting these loops, no attempt has been made to preserve in the diagram the natural direction in which the tube is actually bent. However, the relative positions of the bends in an antero-posterior direction have been accurately reproduced.

In the younger individuals of this stage, the pronephros (Fig. 58) resembles in many respects that of Rana represented in Figure 33; but it differs from the latter, notably in the occurrence of two instead of three nephrostomes and nephrostomal canals. For this reason, there is no canal which corresponds to the collecting trunk of Anura, save that

portion of the latter which intervenes between nephrostomes I. and II.; and in discussing the topographical relations of the tubules it will be needless to distinguish this remnant of the collecting trunk from the first nephrostomal tubule. In this simplest condition of the pronephros, the common trunk makes a single loop, the anterior curve of which is situated nearly as far forward as the level of the first nephrostome. In somewhat older pronephridia (Figs. 59, 60) the main bend of the common trunk occupies a position even in front of the first nephrostome, and a number of minor folds intervene between the junction of the nephrostomal canals and this most anterior fold. In none of the pronephridia of this stage is there any evidence of convolution in the nephrostomal canals.

One individual of this stage departed from the normal condition, in that it possessed three instead of two nephrostomal canals. This abnormality occurred on both sides of the body, and appears to be correlated with a less highly developed first nephrostomal tube. It is to be noted that the third tubule (Fig. 57) appears as an appendage attached to the most posterior loop of the common trunk. This topographical relation suggests that it is the most posterior of the three nephrostomal tubules which has been added to those normally present in Amblystoma, and this inference is shown to be correct by the relations which the several tubules bear to the body somites. The question whether the most posterior of the three tubules in this case represents the third nephrostomal tubule of the *Anuran* pronephros can be answered only by a consideration of the relations which the several nephrostomes in the two groups bear to the overlying protovertebræ, and will be recurred to in the general discussion which follows. I may here anticipate to the extent of stating that the first and second tubules of Amblystoma probably correspond respectively to the second and third of Rana and Bufo, the abnormal third tubule belonging to a yet more posterior metamere.

The position of the pronephric nephrostomes with reference to the myotomes was determined at an early stage by the location of the first metameric diverticula which are developed within the pronephric mass; and in the present stage these relations have not materially changed. The two nephrostomes of the normal pronephros lie beneath the third and fourth myotomes respectively. In the case of the pronephridia with a supernumerary nephrostome, the first two nephrostomes occur beneath myotomes III. and IV. respectively, while the third nephrostome is found beneath myotome V.[1]

[1] Myotome I. of this enumeration reaches forward to the root of the vagus nerve, and is flanked on its outer face by a portion of the ganglion nodosum, exactly as in the case of the Anura described.

In this stage the segmental duct in the younger embryos shows somewhat different conditions from those found in the older embryos. In the case of unhatched embryos possessing the simple pronephros shown in Figure 58, the duct on passing backwards gradually diminishes in calibre, and finally loses all trace of a lumen. The fundament of the duct is in this region composed of four or five cells in each cross section, which are frequently arranged with some regularity about the centre as an axis. On proceeding to more posterior regions the fundament of the duct becomes intimately connected with the mesoderm, and is finally lost in that layer. In Amblystoma the histological characters of the mesoderm and the ectoderm are not sufficiently unlike to allow one to base on them a definite conclusion respecting the layer which has furnished the material for the fundament of the duct. In all cases which I have observed, however, the duct neither unites with the ectoderm nor terminates freely; but its posterior end invariably is closely applied to the mesoderm, and consequently is most probably derived from that layer. In view of the fact that the yolk spherules of the fundament of the duct are of the same size as those present in the adjacent mesoderm, I am of opinion that the duct has undergone no extensive independent growth, but has arisen *in situ* as a proliferation of the somatopleure.

In the older embryos of this stage, the duct has extended backwards to the region of the cloaca, and joins the latter near the posterior face of myotome XX. A distinct post-anal gut is present at this stage. Its anterior portion contains an evident lumen, and appears as a direct continuation of the pre-anal portion; its posterior tip is solid, and extends backward into the tail region for the distance of about one millimeter. From the ventral floor of this continuous intestinal tube, a median diverticulum leads backward and downward to the anus. The histological characters of this diverticulum differ markedly from those of the rest of the intestine, and by comparison with younger stages it becomes evident that the former has resulted from a proctodæal invagination. Where the intestinal tube is joined by the proctodæum the ventral portion, or cloaca, is T-shaped. The lateral arms receive the segmental ducts, and the ventral stem may be followed to the anus. In Amblystoma, then, the segmental ducts open into the intestine at the point where the proctodæal ectoderm and the entoderm pass over into each other. It is somewhat doubtful with which of the two germ layers the wall of the ducts becomes continuous; but it is possible that — in contrast to the condition obtaining in the Anura studied — the ducts open upon an ectodermal surface.

In the younger embryos of this stage, the walls of the pronephric tubules are all very thick; they gradually diminish in thickness as the embryo grows older. The lumen, on the other hand, is at first narrow, but afterwards becomes much wider. Its size varies greatly in different portions of the pronephros. For example, the lumen of the long arm of the common trunk, which forms the direct continuation of the segmental duct, is usually much narrower than the average lumen of the other pronephric tubules. The nephrostomal canals near their junction and the adjacent portion of the common trunk usually have a wide lumen. In the abnormal pronephros represented in Figure 57, however, the lumen of the first nephrostomal tubule was very narrow, a circumstance which, as I have already suggested, may possibly be correlated with the presence of a third nephrostome.

The lining epithelium of the tubes is composed of polygonal cells, which in the younger embryos have a high columnar form, but become gradually thinner as development proceeds. The nuclei when stained with Czokor's cochineal show a coarsely granular or reticulate structure, and are located close to the lumen of the tubule. The protoplasm takes a uniform delicate tint, which is masked, however, by the deeply staining yolk spherules. These are most abundant near the basal surface of the cell; they decrease in number and in size with the growth of the larva.

In the younger embryos of this stage, the somatopleure is composed of somewhat flattened cells, whose superficial dimension is approximately double the thickness of the cell. The walls of the pronephric tubules in these embryos have a thickness of about 37.5 μ, while the parietal peritoneum has an average thickness of only about 15 μ. These two epithelial layers are confluent at the nephrostomes, the wall of the tubule diminishing rapidly in thickness to that of the peritoneum. The nephrostomes, as well as many of the pronephric tubules, are slightly pigmented on their internal surfaces; but the pigmentation is by no means so conspicuous as in Rana and Bufo. In the older larvæ of this stage, the peritoneum is much thinner; but since the walls of the tubules have also diminished in thickness, nearly the same relations are to be observed at the nephrostome as in the younger embryos.

As in Rana and Bufo, the pronephric capsule in Amblystoma develops in the form of a downgrowth from the somatic layer of the protovertebræ. In Amblystoma the two-layered condition of the capsule and its connection with the overlying protovertebræ are maintained in the oldest larvæ of this stage. It seems probable, moreover, that the downgrowth from the protovertebræ is met by a more or less pronounced

upgrowth from the somatopleure immediately ventral to the pronephros. The thickness of the capsular sheath gradually diminishes in the course of the development of the larvæ, but it is in general approximately equal to that of the peritoneum in the same individual. In the older larvæ, moreover, the pronephros, and especially the segmental duct, become partially covered by a downward extension of the myotome. In such larvæ the anterior limb bud is prominently developed at this stage, and its cells cover in part the posterior ventral portion of the pronephros.

The sinuses within the capsule are bounded by mesenchymatic cells and contain scattered blood corpuscles; they are continuous posteriorly with the posterior cardinal veins, so that the venous blood in passing forward from the hinder portions of the body bathes the pronephric tubules on every side.

The vessel emerging from the anterior end of the pronephros receives a large vessel from the head, and from the point of union the ductus Cuvieri leads to the sinus venosus. The former vessel is one of the jugular veins. The distribution of this vein and its probable representative in the adult will be considered in connection with the following stage.

The first trace of the glomus appears in embryos of this stage. It consists, as in Rana and Bufo (compare Plate I. Figs. 8, 9, and Plate VI. Fig. 47), of a horizontal fold of splanchnopleure lying close to the dorsal angle of the body cavity. This fold extends, when fully formed, from the first nephrostome backwards to the second. The outer layer of the organ consists, as shown by its development, of splanchnic peritoneum, which is usually bounded within by a sharp contour. I am of opinion that the latter is in reality a thin structureless basement membrane. The interior mass of the glomus consists of several different elements. In the young stages embryonic blood cells form a prominent constituent. Other cells are present, which have an elongated form and are evidently connective-tissue elements; and there appear to be still other cells which are of a less modified character and in which nuclear mitoses occur. Many of the latter may well represent young stages in the development of blood corpuscles, for I have observed mitotic division of blood cells even in certain older larvæ of Stage VI. In addition to the classes of cells just mentioned, there are a few large cells whose nature is to me quite obscure. These cells measure 60 μ or more in diameter, and contain large yolk spherules, which are closely packed together and make up almost the entire substance of the cell. The histological characters of these cells ally them most closely with those of the entoderm, and in the youngest stages in which I have been able to identify

them they were closely associated with the yolk entoderm, which lies medio-ventral to the region of the glomus. It is probable that they arise from the entoderm and migrate into the interior of the splanchnopleural fold. I have been unable to find in either Rana or Bufo any cells similar to these large cells in the glomus of Amblystoma, and I have at present no suggestion to offer respecting their significance. The glomus, as I have already indicated, is a highly vascular organ, and even in the younger stages it is possible to find vessels which connect it with the aorta. These vessels usually follow the splanchnic layer quite closely, and appear to lie external to the large cells to which reference has been made.

In the younger larvæ of this stage the body cavity in the pronephric region has the form of separate chambers, from each of which a single nephrostomal tubule arises; but elsewhere the cavity is wanting on account of the contact of the peritoneal surfaces. In the older individuals it is expanded over a much larger area, but by the development of the lung bud a dorsal portion of the cavity is partially separated from the rest as a pronephric chamber.

Stage VI.

Plate VII. Figs. 53, 54. Plate VIII. Figs. 61-65.

The larvæ included in this stage were taken from several different killings made in the course of three or four days. They measure about 9 mm. from the anterior end to the tip of the tail. An anterior limb bud is plainly visible upon surface view, and the tail is provided with a distinct membranous fin.

The great complication in the structure of the pronephros which is attained in this stage is accomplished by a continuation of the same process of forming convolutions that has been described for the preceding stage. Indeed, the separation of the two stages is at best quite arbitrary. Figures 61–65 represent various pronephridia of the present stage. It is to be noticed that the portion of the common trunk of which the segmental duct is the direct continuation can be traced from the anterior limit of the pronephros backwards without convolution, or after having formed a few insignificant loops. The common trunk from its junction with the nephrostomal tubules to this most anterior bend is thrown into a series of complicated convolutions, which may be so arranged as to present a gradation of considerable regularity (Fig. 62), or may be quite irregular (Fig. 65). In most cases, however, it is to be noticed that the arrangement of the loops is in general favorable for a compact

disposition of the tubes (Fig. 62). The convolution in this stage is no longer confined to the common trunk, the nephrostomal tubules undergoing slight contortion (Figs. 63–65).

I have determined the positions of the pronephric structures to the somites in these later stages by their relations to the spinal ganglia. The first and second nephrostomes lie very nearly in the same transverse plane as the first and second spinal ganglia respectively. In the youngest larvæ of this stage the boundaries between the myotomes may still be made out in transverse sections, and the nephrostomes are then found to lie beneath myotomes III. and IV. It is probable that in later stages as well two myotomes occur in front of the first spinal ganglion.

The duct after leaving the pronephros pursues a nearly straight course backwards to the cloaca. In the larvæ of this stage, the post-anal gut has atrophied, and the ducts open into the intestinal tract just at the point where it bends downward toward the anus or cloacal aperture. The outlets of the two sides of the body are quite widely separated, never opening into an unpaired median depression in the dorsal roof of the cloaca, as is the case in the corresponding stage of Rana. The outlets of the segmental ducts are situated between the eighteenth and the nineteenth spinal ganglion, which would correspond to somite XX. or XXI. Their position is, then, the same as in the preceding stage. (Compare page 254.)

In the series of embryos included under Stage V., it was shown that the walls of the pronephric tubules became gradually thinner as the animal developed. In the pronephridia of the present stage the same process has been continued, and the cells are frequently so reduced in thickness that the nucleus appears to be in contact with the basal as well as the superficial, or inner, surface of the cell. Occasionally tubes occur whose walls are so thin that each nucleus causes a protuberance into the lumen of the tube. But wherever the thickness of the epithelium exceeds the diameter of the nucleus, it is to be noticed that the latter lies close to the inner surface of the tube, whereas the yolk spherules are accumulated in the basal portions of the cells. The yolk spherules are much less numerous than in the preceding stage. In many cells they are wholly wanting, and in all they now form a much less prominent constituent than the cell protoplasm.

The nephrostomes present no new features of interest in this stage. Most of the pronephric tubules contain more or less pigment, which is usually accumulated in irregularly distributed dark patches. In one or two instances I have had a fair degree of success in dissecting out the

pronephros of a fresh specimen. In such an isolated pronephros the course of the tubes can be followed with tolerable accuracy in consequence of the pigmented areas occurring in their walls. The loss of yolk spherules, to which the pronephric tubes have been subjected on reaching the present stage, is shown in a striking manner by the transparency of the gland as contrasted with the snow-white yolk-entoderm.

The histological characters of the duct (Plate VII. Figs. 53, 54) resemble closely those of the pronephric tubules. Its calibre is greatest in the region immediately posterior to the pronephros (Plate VII. Fig. 54), becoming less as the duct passes posteriorly (Fig. 53). Throughout its course it is accompanied by the posterior cardinal vein (*vn. crd.*). In the older larvæ of this stage, the segmental duct in its passage backwards to the cloaca receives a large number of mesonephric tubules, which will be described in the sequel.

The pronephros of the present stage is covered on its dorsal surface by the main body of the myotomes. From the outer angle of each myotome, moreover, a distinct fibrillar sheet envelops the entire lateral surface of the gland. This layer is the capsule, whose origin has been discussed in connection with Stage V. In the present stage, it frequently becomes deeply pigmented.

The anterior portion of the pronephros is also overlaid by a stratum of smooth muscle fibres, which arises from the dorsal fascia. This muscular sheet is continuous in front with a muscle layer which is inserted upon the ventral surface of the mandible, and probably represents the depressor maxillæ of the adult.

The pronephros is also covered in part by the shoulder girdle, which in this stage is wholly composed of cartilage.

The vascular sinuses enclosed within the capsule are the direct continuations of the posterior cardinal vein. They also receive — usually about midway between the first and second nephrostomes — a blood-vessel, which may be traced nearly as far back as the cloaca, and which accompanies in its course the ramus lateralis of the vagus nerve (see Fig. 53, just median to *n. l.*). I am not aware of any prior mention of a vessel having this course, and am unable to state whether this vein has any representative in the adult.

The vessel emerging from the anterior end of the pronephros receives a vessel from the head, and the two form the ductus Cuvieri, which proceeds downward and inward to join the sinus venosus. The anterior branch may be traced forward into the head in the same direction as the original trunk ; it accompanies in its course the ramus lateralis vagi.

In consequence of the uncertainty as to what vein of the adult this vessel represents, I shall here digress to describe its distribution at this stage. For purposes of description, I shall follow it from its point of junction with the cardinal vein forward towards its finer branches. Before reaching the ganglion nodosum, it sends a branch dorsalward, which can be traced for a short distance between the lateral wall of the cranium and the ganglion. The main trunk continues forward external to the ganglion, and gives off a branch which passes around the posterior end of the auditory capsule and enters the cranium. The original vessel now passes forward through a narrow channel left between the auditory capsule and the articulating portion of the mandibular cartilage. Near the anterior end of the auditory capsule it divides into two branches, one of which passes dorsal to the eyeball, accompanying in its course the ophthalmic branch of the trigeminal nerve; the other branch passes ventral to the eyeball, and continues into the anterior maxillary region, following the course of the canalis nasalis. The main trunk runs nearly parallel to the aortic root and its prolongation, the carotid artery, the efferent branchial trunks joining the aortic root by passing immediately ventral to the vessel whose course I have been following. The vein evidently corresponds to the one described under Stage V. of Rana (page 233, foot-note), and appears to me to represent in all probability the internal jugular of Gruby ('42) and of Ecker ('64–'82).

The glomus is considerably broader and thicker than in Stage V.; but its longitudinal extent is about the same. In the middle of its course its distal edge reaches across the body cavity and fuses with the somatic peritoneum which covers the pronephros. The structure of the organ appears to be nearly the same as in the preceding stage, but the interior mass is so compact that one can distinguish little more than the nuclei, which present quite uniform characters. Cells which are unquestionably endothelial are frequently evident along the basal surface of the peritoneal layer; they also traverse the interior of the glomus dividing this space into compartments. Pigment is present both in the peritoneal wall and in the interior mass. It has a scattered distribution, appearing in the form of perfectly black patches. The large cells to which allusion was made in Stage V. are present also in this stage. They have about the same size and histological features that formerly characterized them. The pronephric chamber has not changed materially from the condition exhibited in Stage V. The most anterior pronephric tubules are situated immediately lateral to a diverticulum of the body cavity, which in sections through this region appears wholly isolated. On following the

series of sections backward, however, the chamber enlarges greatly, even before the nephrostomes are reached, and is separated from the ventral portion of the body cavity only by the lung bud. Between the first and second nephrostomes, the pronephric chamber is divided into two parts by the fusion of the distal edge of the glomus with the somatic peritoneum covering the pronephros. Still farther posteriorly, an open communication is established, not merely between these two portions of the pronephric chamber, but also between the latter and the general body cavity.

In almost all the larvæ of this stage, the mesonephric tubules have appeared, and in many individuals they have already opened into the duct. There is always a space intervening between the pronephros and the mesonephros, in which no tubules are developed. This interval appears to be subject to some variation, but in the majority of cases it comprises four somites.

In the most anterior region of the mesonephros the tubules show traces of a metameric arrangement, but this is wholly lost in more posterior regions. These relations can perhaps be best illustrated by the accompanying table, which shows the positions of the right mesonephric tubules in the larva, whose pronephros is represented in Figure 64. The somites have been reckoned by reference to the spinal ganglia, but the results are here expressed in terms of the original metamerism of the myotomes.

Somite	III. — Pronephric nephrostome I.
"	IV. — " " II.
"	V. — Tubules absent.
"	VI. — " "
"	VII. — " "
"	VIII. — " "
"	IX. — 1 mesonephric tubule.
"	X. — 1 " "
"	XI. — 1 " "
"	XII. — 2 " tubules.
"	XIII. — 3 " "
"	XIV. — 3 " "
"	XV. — 4 " "
"	XVI. — 5 " "

Each tubule of the mesonephros (Plate VII. Fig. 53) has the ordinary form, which has induced several authors to call it "sickle-shaped," and consists of cells which are wholly devoid of yolk spherules, in which the nucleus occupies almost the entire body of the cell. Along the region which corresponds to the cutting edge of the sickle, a few loose cells (*fnd.*

glm.') occur, which constitute the earliest fundament of the glomerulus. The nephrostomes, however, have not opened at this stage.

In the region between pronephros and mesonephros (Plate VII. Fig. 54) certain masses of cells are found on the median side of the duct in the same position as that occupied in the posterior region by the mesonephric tubules. These cells do not form a continuous mass, but are interrupted at intervals. The cords of cells thus formed do not, however, appear to correspond in their arrangement to the metamerism of the body. It is possible that they represent rudimentary nephridial tubules, but the evidence in favor of this interpretation must be regarded as far from satisfactory.

I have been unable to ascertain the precise mode of origin of the mesonephric tubules, having sought in vain for nuclear mitoses which should throw light upon this question. There are in younger stages many retroperitoneal (subperitoneal) cells which might be collected and rearranged so as to produce the tubules; or, again, the fundaments of the tubules might be formed by proliferation from the peritoneum. The cells of the tubule have evidently undergone very rapid division, as is indicated by the complete consumption of the yolk; and this circumstance seems to me to favor the second view. Furthermore, I have found nuclear mitoses (Fig. 54) in the region immediately in front of the mesonephros which indicate that the cords of cells in this region arise from the peritoneum. Although I am unable to assert that the mesonephric tubules arise from the peritoneum, I am inclined to regard it as probable that they do. There is no evidence, however, of a definite invagination of the wall of the body cavity.

This is the oldest stage of Amblystoma which I have examined, and with it I close the descriptive part of this paper.

III. General Discussion.

Having presented in a purely descriptive manner the facts of development as yielded by my own studies, I shall now endeavor to use these observations as a basis for the criticism of the results of other investigators, and in closing shall point out certain general conclusions which seem to me warranted by such a review.

Recent researches have extended greatly the number of animals in which a homologue of the pronephros is known, so that it may now be fairly assumed that the organ appears in the ontogeny of all Vertebrates.

In view of much recent evidence (Hatschek, '88[b], Rabl, '88, Ayers, '90)

which clearly supports the view that Amphioxus is closely related to Craniotes and occupies a position near the base of the Vertebrate phylum, the kidneys of this animal are of prime interest in the present connection. Notwithstanding the extreme importance of the subject, however, the relation of the excretory system of Amphioxus to other Chordates must still be regarded as a matter of considerable doubt.

At least seven different views have been advanced respecting the excretory organs of this animal. According to the earliest of these views, which originated with Joh. Müller ('42, p. 101, see also Langerhans, '76, p. 322, and Rolph, '76, p. 140), certain modified groups of cells lying in the posterior portion of the atrium are claimed to possess an excretory function. I presume that no morphologist would endeavor to homologize these excretory patches with the kidneys of Vertebrates. The same is true of the glandular structures described by Owen ('66, p. 533, Fig. 169, *h*), and the epithelial bands of Wilh. Müller ('75, p. 109). Nor can I see in the "pigmented canals," atrio-cœlomic funnels, of Lankester ('75, pp. 260, 261, and '89, pp. 394–397) any features which would definitely link them to Vertebrate nephridia.

The account given by Hatschek ('84) of his discovery of a single nephridium, which he believes to open into the pharyngeal cavity, is too brief to permit one to form a final judgment upon his interpretation. The observation has not been confirmed by any subsequent investigator save perhaps Lankester and Willey ('90, p. 459), who do not however regard this organ, which they call the sub-chordal tube, as a nephridium. There is nothing in its structure as described by either author which in my opinion justifies its comparison to a Vertebrate excretory tubule.

The most recent paper on this topic, which is by Weiss ('90), is of considerable interest from the physiological researches which it records: these show that a large portion of the atrial epithelium, as well as the excretory patches of Müller, have a well marked excretory function. Of greater morphological value is the description given by Weiss of certain small tubules in which the excretory function is peculiarly active. These tubules empty into the atrium at the upper margin of that cavity in the region of each secondary gill bar. They seem to project into the cœlom, but Weiss was unable to detect a continuity between their lumen and the cœlom. Since the relations of these tubules to the cœlom are not ascertained, I am of opinion that the observations of Weiss do not afford satisfactory reasons for regarding them as homologues of either the Vertebrate or the Annelidan nephridia. Weiss's account, however, is at least very suggestive. An important feature is the metamerism of the

tubules; for while the metamerism of the gill bars does not correspond in the adult to that of the myotomes, yet we should not lose sight of the fact that according to Kowalewsky ('67, see his Figs. 36 and 39) such a correspondence exists in the embryo. At such a stage, then, there would be present a single excretory tubule for each myotome.

In a recent lecture before the Gesellschaft für Morphologie und Physiologie in München, Boveri ('90) has endeavored to show the existence in Amphioxus of homologues of the pronephros, the mesonephros, and the segmental duct. The tubules which Boveri regards as pronephric are probably the same structures as the excretory tubules of Weiss; and I infer that the same have been seen by Spengel ('90, p. 282), though this writer makes no suggestion as to their significance. Both Weiss and Boveri claim to have proved by feeding the animals with carmine that the tubes are actually excretory. According to Boveri, also, they open into the atrium at the upper margin of each secondary gill bar; but their course is somewhat differently described by the two authors. Boveri maintains that each tube communicates by means of several openings with the dorso-pharyngeal cœlom. As confirmatory of his position that these canals represent the pronephric tubules of Craniota, he describes the relations they bear to the gill vessels, which he identifies with the segmental vessels described by Paul Mayer ('87, p. 343) in Selachii. According to Rückert ('88, pp. 239–242), the glomus of Elasmobranchs consists of a rete mirabile in connection with these segmental vessels. Adjacent to the excretory tubules, Boveri finds that the gills display an increase in vascularity, and that anastomoses are formed between the branchial vessels. This condition does not seem to have been noticed by Weiss. Spengel, who made a special study of the gill vessels, describes a longitudinal vessel at a corresponding level (longitudinal trunk of the ligamentum denticulatum), but does not discuss its significance. It seems to me that Boveri's observations, provided they be confirmed, afford fairly satisfactory evidence of the existence of true nephridia in Amphioxus; and, as I shall endeavor to show in the sequel, that these are constructed on a type which may be assumed to represent a primitive condition of the Vertebrate kidney.

The starting point of Boveri's researches was the hypothesis that the atrial cavity and gonadial pouches of Amphioxus correspond to the segmental duct and mesonephros respectively of Craniota. The attempts of Haeckel ('74[a], p. 37, and '74[b], p. 305) and of Huxley ('76, pp. 221, 222) to discover a homologue of the segmental duct in Amphioxus must, in my opinion, be held to have at present merely an historical interest;

it remains for me to consider whether the theory of Boveri be better grounded.

The arguments which are adduced in favor of the homology of the gonadial pouches and the mesonephros may be reduced to the following points of similarity. The gonadial pouches of Amphioxus are metameric diverticula of the dorso-pharyngeal cœlom, in accordance with the established views of Kowalewsky and Rolph, as confirmed by Boveri, who finds in the adult a continuity of the epithelia belonging to the two tracts; the mesonephric tubules likewise are primitively metameric diverticula from the dorsal portion of the body cavity (see Sedgwick, '80[a], *et al.*). The generative cells develop in the walls of the gonadial diverticula; the early occurrence of germinal cells at the proximal ends of the forming mesonephric tubes has also been described by Rückert ('88, p. 257) for Selachii. Finally, the canal by which the gonadial pouches primitively communicated with the cœlom arches over the dorsal angle of the atrial cavity in a way that is very similar to that in which the mesonephric tubules curve outward to join the duct. The only reason — save those that require the prior assumption that the gonadia represent mesonephric tubules — which I can see for identifying the atrium with the segmental duct is the fact that nephridial (pronephric?) tubes open into it. This argument seems to me of very little weight. Boveri himself believes that the pronephros primitively opened directly to the exterior. Unless other evidence can be adduced, I see no adequate reason for regarding the formation of the atrial cavity as a step in the development of the segmental duct. On the other hand, that interpretation seems to me quite opposed to all that is known of the development of the segmental duct. As I have shown in the preceding pages, there can be no doubt that, in Amphibia at least, the duct develops solely from the mesoderm. According to the opposed view — the ectodermal origin of the duct — the development always proceeds from a *pair* of narrow rod-like thickenings of ectoderm, one on each side of the body, which are very different from the *unpaired* ventral groove from which, according to the most recent account (Lankester and Willey, '90) the atrium develops. If, now, we deny the homology of the atrium with the segmental duct, the outward arching of the gonadia becomes a most insignificant topographical resemblance. It seems to me that it would be manifestly unfair to base so far reaching a homology on the remaining points of resemblance, viz. the early occurrence of germinal cells in the mesonephric tubules, and the circumstance that the gonadia are metameric diverticula of the dorso-pharyngeal cœlom.

Turning now to Craniota, the pronephros in Amniota and Selachii is a wholly degenerate structure; in many Anamnia, however, it serves for a longer or shorter time as a functional excretory organ.

The pronephros of Dipnoi alone is wholly unknown. Beard ('90, p. 157) speaks of the transformation of a part of the pronephros into the Müllerian duct as "a well known fact"; but the only authority he cites in this connection (Parker, '89) does not make such a statement, nor have I succeeded in finding anywhere in the literature any account of the pronephros of Dipnoi. Unless Beard has personal observations on this matter, I believe that in Dipnoi absolutely nothing is known of the pronephros or its transformation, save such inferences as may be drawn from the adult anatomy. I shall therefore merely repeat the statement of Ayers ('85, p. 506), that the development probably proceeds as in Amphibia, since the adult urogenital system in this group presents the closest analogy with that of the Dipnoi.

The excretory system of Cyclostomes is similar to that of Amphibia. In Petromyzon a pronephros develops in the Ammocœtes larva, but aborts in the adult. The number of nephrostomes and of tubules is small (4, according to Wilh. Müller; 4 to 5, Shipley; 3, Kupffer; according to Semon, an inner and an outer row of nephrostomes are to be distinguished); and they communicate with an anterior expanded portion of the body cavity. According to Fürbringer ('78[a], p. 42), the pronephros extends over about four somites. Opposite the nephrostomes, a vascular organ projects from the root of the mesentery into the body cavity. This is the so-called glomerulus; as figured by Scott ('81, Taf. IX. Fig. 24), it strikingly resembles the glomus of Amphibia. According to Scott, the pronephric tubules develop secondarily as outgrowths from the segmental duct. On the other hand, Shipley has confirmed the statements of Müller and Fürbringer, according to which the nephrostomes and tubules are formed by the incomplete closure of a longitudinal groove of somatopleure. Finally, Kupffer maintains that the tubules arise as *three separate evaginations of the somatopleure*, a result which is in harmony with my own observations on Amphibia.[1]

In Myxine nothing is known of the early development; but in late stages an organ has been made known by the studies of Wilh. Müller

[1] In Goette's ('88, p. 163) preliminary account of the development of Petromyzon he states that a pronephros develops in the *same* manner as in Amphibia. This would indeed be a conclusion acceptable to me, but until the accounts are more at one in regard to the latter group the statement is somewhat vague. I await with interest the publication of that portion of Goette's final paper which relates to the excretory system.

('75) and of Fürbringer ('78ª, pp. 38, 39), which plainly represents the Amphibian pronephros. Whether it ever persists in the adult is still a matter of doubt (see Weldon, '84) ; but in young individuals, at least, the segmental duct (ureter) is prolonged anteriorly to the heart region. Here it gives off numerous coiled tubes, which branch and open by funnel-shaped nephrostomes into the pericardial cavity. On its dorsal side, the duct gives off a few tubules which terminate in glomeruli resembling those of the mesonephros. This condition and the large number of tubules constitute the main points of difference between the Amphibian pronephros and that of Myxine.

The pronephros of Teleosts and Ganoids appears to me to be reducible to a single type of structure, which can be easily derived from the condition present in Amphibia and Cyclostomes (and Dipnoi ?). The so-called head-kidney of Teleosts described by Hyrtl ('51, p. 29) is probably derived from the embryonic pronephros, though mesonephric elements may also be found in the adult head-kidney (see Emery, '82, p. 46).

According to Rosenberg ('67, pp. 42 *et seq.*) and Oellacher ('73, pp. 97–100), the excretory organs arise as a pair of grooves of the somatopleure directly beneath the protovertebræ. A process of constriction, which proceeds from a middle region forwards and backwards, leads to the conversion of each groove into a tube, the segmental duct. The anterior portion becomes wholly cut off from the body cavity, and is thrown into numerous coils. The tip becomes considerably swollen, and is invaginated by an outgrowth from the aorta forming a single glomerulus on each side.

Goette's ('75, pp. 826, 827) account of the development of the pronephric glomerulus in Teleosts is somewhat different, and affords a better basis for homologizing the pronephros of Teleosts with that of Amphibia. Goette maintains that the somatopleural groove is imperfectly closed in front, leaving a single nephrostome, opposite which a glomerulus (glomus) is developed. Subsequently, the pronephric chamber becomes separated from the rest of the body cavity, and comes to resemble a Malpighian capsule with its contained glomerulus. While Fürbringer ('78ª) confirms Goette's view, Hoffmann ('86, p. 621 *et seq.*) has quite recently reasserted that this Malpighian capsule is the blind infolded end of the segmental duct, and the homology with the Amphibian glomus and pronephric chamber, which appears to me probable, he denies. Hoffmann's position does not seem to me tenable in the light of comparative studies. Even though it should be shown that the ducts

have absolutely no connection with the body cavity at the time when the glomerulus is formed, I could nevertheless defend my position by the assumption that the blind anterior end of the duct is a compound structure, representing both nephrostomal canal and pronephric chamber. It seems to me that, were it necessary to make this assumption, an extensive comparative study would justify such an interpretation.

The pronephros of Teleosts was long supposed to remain functional in the adult; but recent investigations seem to favor the conclusion that it never persists in fully mature individuals, with the possible exception of a few degenerate animals like Fierasfer (cf. Balfour, 81[b], '82; Grosglik, '85 and '86; Emery, '80, '81, and '85; Calderwood, '91).

The account given by Balfour and Parker ('82, pp. 415–424) of the development of the pronephros in Lepidosteus is in very close agreement with the development in Teleosts as described by Goette and by Fürbringer. The only conspicuous point of difference is, that, while in Teleosts the pronephric chamber becomes wholly detached from the body cavity, in Lepidosteus a remnant of the original communication probably persists as a so-called peritoneal tubule. As among Teleosts, the pronephros atrophies in adult Lepidostei.

Beard's ('89, pp. 114, 115) account of the early development differs greatly from that just given. According to this author, the pronephros is formed as a solid proliferation from the intermediate cell layer (Balfour) in the region from the 4th to the 8th or 9th somite inclusive. Externally, the proliferation fuses with the ectoderm. As a rule, there are formed three pairs of pronephric nephrostomes, of which the most posterior pair abort. The pronephric chamber is formed by the narrowing of the ciliated opening and the widening of the part opposite the glomerulus. Since Beard does not describe the development of the glomerulus, the account seems to me decidedly vague; but I believe I am right in accrediting to the author the view held by Hoffmann for Teleosts, that the glomerulus is not developed in the body cavity. As I understand him, it is developed in the course of the pronephric tubes.

All the studies on Ganoids thus far enumerated have been made upon Lepidosteus. In Acipenser, Salensky ('78, '80) maintains, in opposition to Kowalewsky, Owsjannikoff and Wagner ('70), that the excretory organs first appear as a differentiation in the form of a solid cord of cells. There is at that stage no trace of the cœlom, nor of a division into protovertebral and lateral plate. Indeed, this cord of cells first marks the region where the latter separation will later occur. In its further development the

cord of cells acquires a lumen, either by a rearrangement of the cells, or by destruction of the axial ones. Anteriorly the structure now opens into the body cavity. The anterior portion elongates and becomes more and more convoluted up to the time of "post-embryonic" development. Opposite each of the peritoneal funnels are formed glomeruli [glomi] as processes from the radix mesenterii. They are covered by a pigmented layer of peritoneum. Salensky does not seem to me to have been very clear upon the earliest development, which was studied mainly by surface views, and I am of opinion that these stages would show very different conditions if more recent technical methods were employed. The most interesting feature of the development, as described by Salensky, is the occurrence of a glomus in the position which is typical for Amphibia and Petromyzon.

The excretory system has probably been studied more carefully in Selachii than in any other group. The independent researches of Balfour ('75 and '78) and Semper ('74 and '75) are in substantial accord, and have formed the basis for all subsequent investigations. For our purpose, the most prominent feature of the development as described by these authors is the absence of any structure which demonstrably represents the pronephros. According to Balfour, the first trace of the excretory system appears as a solid knob springing from the "intermediate cell mass" near the level of the hind end of the heart. From this anterior proliferation a solid cord of cells grows backward between ectoderm and mesoderm. The posterior portion is the fundament of the segmental duct; the anterior knob persists in adult females as the ostium abdominale of the oviduct. According to Balfour, this solid knob represents a rudimentary pronephros.

Very recently the early development of the excretory organs has been placed in a new light by the researches of Rückert ('88) and van Wijhe ('89). According to Rückert, the development begins with the formation of a pronephros as an outgrowth towards the ectoderm from the ventral portions of several *protovertebræ*, extending from the third or fourth trunk somite backwards for a distance of four to six somites. The thickening extends ventrally in each somite to the region where the segmented mesoderm passes into the unsegmented lateral plates. The proliferation, in the formation of which the somatic layer is alone concerned, shows on careful study a metameric character. From the posterior end of each protovertebra a narrow canal can be traced outwards and backwards, where it unites with a similar canal emerging from the next following somite. The pronephric mass fuses for a time with the

ectoderm and probably receives a contribution of cells from that layer. The duct grows backwards as far as the cloaca at the expense of the ectoderm. Having reached this stage of development, the pronephros rapidly degenerates. This process takes place in a slightly different way in the anterior and posterior regions. A variable number of the most anterior evaginations flatten out into a simple longitudinal groove of peritoneum, the ostium abdominale; the remaining ones become closed and detached from the peritoneum; thus there remains a longitudinal canal communicating with the body cavity by the slit-like ostium. In interpreting the structure as a rudimentary pronephros, it is important to note the discovery by Rückert (pp. 239–242) of a structure which he regards as a pronephric glomerulus, or glomus. This structure is developed in connection with segmental blood-vessels which pass from the aorta to the right subintestinal vein, and which have been described by Paul Mayer ('87, p. 343). In Torpedo the vessels are present on the right side in the same number as the segments of the pronephros, and as they pass ventrally between the entoderm and the splanchnopleure it is to be noticed, in regard to the middle vessels at least, that they send out buds, which form projections from the median peritoneal wall opposite the pronephric tubules.

It will be at once seen that the development of the pronephros as described by Rückert is in striking agreement with the account I have given of the early stages in the development of the Amphibian pronephros, and I have no hesitation in homologizing the two organs. The earliest stage which has been observed in both groups is that which I have termed the pronephric thickening. This is followed in both by the stage of canalization; but the Selachian pronephros never goes beyond an early condition of the pronephric pouch, in which, however, the homologues of the nephrostomal tubules and the collecting trunk appear. The points of difference between the account I have given and that given by Rückert for corresponding stages of the Selachian pronephros seem to me, with a single exception, to be either unreal or insignificant. The exception to which I refer pertains to the participation of the ectoderm in the formation of the pronephric thickening. This condition I am confident does not occur in Amphibia. Moreover, the evidence upon which Rückert bases his statement seems to me far from conclusive, nor has his observation been confirmed by any subsequent investigator. Rückert described the pronephric thickening as a product of the protovertebræ. I cannot admit that this is true for Amphibia; but I believe that our differences of opinion are really due to the fact that we use dif-

ferent criteria for determining the boundaries of the protovertebræ. There can be no doubt that the earlier pronephric thickening is made up of metameric constituents; but I should be unwilling to regard all segmented mesoderm as belonging to the protovertebræ. On the contrary, I am of opinion that the ventral extent of the protovertebræ is for the first time defined when the longitudinal constriction appears which divides the primitive cœlom into protovertebral cavity and pleuroperitoneal or (secondary) body cavity. When such a definite line of demarcation has been established, the remnant of the pronephros in Selachii, as well as the functional pronephros in Amphibia, remains connected with the latter space. The remaining points of difference relate to the number of tubules involved, — which, as we have seen, varies even within the class of Amphibia, — and to their position with reference to the somites. The latter feature seems to me to be at once difficult to determine and of minor importance.

Before the conclusion of this paper I shall endeavor to indicate how the glomus of Amphibia may possibly have been derived from the type of structure which is described by Rückert for Selachians and by Boveri ('90) for Amphioxus.

The results gained by van Wijhe ('89) do not seem to me to differ from those of Rückert in many respects which are of importance for a comparative study. The great divergence of their descriptions in the case of many details seems to me to be occasioned mainly by the peculiar conception which Rückert holds of the relations between the protovertebral and the lateral mesoderm. For these details and for the hotly contested questions of priority, I must refer to the original papers (van Wijhe, '86, '87, '88[a], '88[b], '89, Rückert, '88, '89), and consider here those features only which merit special attention because of their bearing on the general questions of homology. Van Wijhe denies positively the participation of the ectoderm in the formation of the pronephric thickening; and he claims that the ostium abdominale is formed from the pronephros by the fusion of the nephrostomes. Finally, structures which are supposed by him (pp. 480–482) to represent the pronephric glomeruli of Rückert are described as occurring on both sides of the body, not, as affirmed by Rückert, on the right side alone, and van Wijhe inclines to the view that they are actually equivalent to the glomi of Amphibia. The body described by van Wijhe consists of a vascular rod, which passes obliquely from the dorsal to the ventral lip of the pronephric pouch, and represents the last trace of the partition between two peritoneal openings, which have not yet fused. Rückert's description is not entirely

clear, and also suffers from misleading typographical and grammatical errors; but it is certain that the structure he describes lies within the splanchnic peritoneum, and is not to be confounded, as was done by van Wijhe, with the partition between two pronephric tubes. Rückert says ('88, p. 239), "Es [ein Paul Mayer'sches Quergefäss] zieht dicht an der medialen Grenze der Vornierenanlage vorbei und gelangt, indem es die Leibeshöhle durchbricht, d. h. ihre Wandung vor sich herstülpt, an die Aussenfläche des Darmes, wo es zwischen Ectoderm [soll wohl Entoderm heissen] und Splanchnopleura gelegen, mit der rechten Subintestinalvene confluirt." I cannot admit that the structure described by van Wijhe is the homologue of the Amphibian glomus, nor do I believe that it corresponds to the structure observed by Rückert.

The mode of development of the excretory system is much alike in the three groups of Amniotes. It seems, however, best in the present instance to deal with the Reptiles separately from Birds and Mammals. The most important of the works on the Reptilian excretory system is perhaps the monograph of Braun ('77), which, however, is of little service in elucidating the earliest stages. Weldon ('83) first gave a satisfactory account of the early development. According to this author, the first trace of the excretory system in Lacerta is found in the region of the intermediate cell mass, and consists of a series of vesicles (Segmentalbläschen of Braun), which have a strictly metameric arrangement. Throughout a region of five protovertebræ (from the 8th to the 12th), there appears on the external wall of these segmental vesicles a rod of cells at first composed of discontinuous parts. This rod is the fundament of the segmental duct; in the region between two successive protovertebræ, it is budded off from the unmodified "middle plate" (Waldeyer), or intermediate cell mass. Behind the twelfth protovertebra, the duct grows backward, free from adjacent tissue. The rod of cells soon acquires a lumen, continuous anteriorly with the cavities of the segmental vesicles.

The observations of Mihalkovics ('85) upon Lacerta agilis differ from those of Weldon mainly in two particulars. In the first place, according to Mihalkovics (pp. 42, 43), the most anterior three or four pairs of segmental vesicles at the time of their origin communicate both with the body cavity and with the protovertebral cavity. In other words, they are formed as expansions of what I have termed the communicating canal, or Mittelplattenspalten of the German authors. Some somites in the series, however, may be without vesicles. Secondly, Mihalkovics (p. 48) maintains that the segmental duct buds off from the middle

plate as a *continuous* cord of cells at a time when only the first trace of the segmental vesicles has appeared. Before the (3 or 4) anterior segmental vesicles have entirely lost their connection with the body cavity, they communicate distally with the lumen of the segmental duct, and may therefore be regarded as typical nephrostomal canals. This condition is never encountered in the posterior vesicles, which develop independently of the cœlom in the solid Wolffian blastema, or middle plate. In consequence of this difference in the mode of development of the anterior and posterior portions, Mihalkovics is of opinion that the first three or four segmental vesicles represent a rudimentary pronephros.

According to Strahl ('86), the segmental vesicles are budded off from the ventral portions of the protovertebræ, and gain secondarily a connection with the body cavity; the duct does not appear until the vesicles are evident.

Ostroumoff ('88[b], p. 81) confirms for Phrynocephalus the observations of Mihalkovics regarding the anterior segmental vesicles, although he is unable to ascertain the precise number that communicate with the body cavity. He also interprets these anterior vesicles as a pronephros. The duct, however, first appears in disjointed fragments lying between successive vesicles.

According to Hoffmann ('89), there develops in Reptiles a pronephros similar to that described by Rückert ('88) for Selachii. It appears as a series of evaginations of the somatopleure. These are formed in the region where the protovertebræ pass over into the lateral plates. The orgar extends over a variable number of somites (6–7 in Lacerta and 5–6 in Tropidonotus). As protovertebræ separate from the lateral plate, the pronephric evaginations remain in connection with the former, except in the case of the first outgrowth (L. agilis, in L. muralis the first two), which forms for a time a single pronephric ostium. The most posterior outgrowth extends backwards, and forms the fundament of the segmental duct. The fate of the several evaginations is different. The most anterior and possibly the next following outgrowth abort at an early stage; the remaining evaginations become detached from the protovertebræ and fuse with one another, thus forming a tube closed in front, but continuous posteriorly with the segmental duct. Hoffmann identifies these evaginations with the segmental vesicles of Mihalkovics and Weldon, but asserts that these authors mistook for a separate fundament of the segmental duct a blind backward prolongation of the evagination belonging to the immediately preceding somite. These backward processes are described by Rückert for Selachii. Ostroumoff's ('88[b], pp. 78, 79) state-

ment, apparently unknown to Hoffmann, that the duct first appears in short fragments, each of which lies posterior to a segmental vesicle, could be readily brought into accord with these observations.

In regard to the correctness of Hoffmann's conclusions that these evaginations represent a pronephros, I am of opinion that there is considerable room for doubt. The organ described by Hoffmann differs in two important respects from that of Selachii, and from the young stages of the Amphibian pronephros as presented in the first part of this paper. In the latter groups, while the metameric evaginations are yet continuous with the cœlom, they have also fused distally to form a longitudinal canal (collecting trunk); this condition I wholly miss in Hoffmann's account, according to which all the evaginations remain distinct from each other till they have entirely separated from the cœlom, and only the more posterior outgrowths ever fuse together. Secondly, no structure comparable to the Amphibian glomus is described. The latter objection would apply equally to the account given by Mihalkovics.[1] None of the previous investigators were more successful in finding glomeruli of the pronephric type.

In regard to the former feature, however, the account of Mihalkovics is more satisfactory, since the most anterior three pairs of vesicles stand in precisely this relation to the body cavity and to the collecting trunk (segmental duct). In reviewing Mihalkovics's interpretation, Hoffmann says ('89, p. 272), since "die Vorniere als eine Ausstülpung, die Urniere nicht als solche entsteht, kommt es mir höchst wahrscheinlich vor, dass die Vermuthung von Mihalkovics, nach welcher die proximalen Urnierenkanälchen der Eidechsen der Vorniere der Amphibien entsprechen, eine andere Deutung zulasse." I judge from this passage that Hoffmann is inclined to regard as mesonephric tubules the anterior three or four segmental vesicles described by Mihalkovics. I am quite unable to harmonize this view with Hoffmann's prior identification ('89, pp. 267, 268) of the pronephric evaginations described by him with the segmental vesicles of Mihalkovics and Weldon. The mode in which the mesonephric tubules develop in Lacerta is asserted to be very similar to that described by Rückert and van Wijhe for Selachii. If I properly understand Hoffmann's description, the space lettered *c.* in Tafel XVII. Figs. 3 and 4, is the lumen of a mesonephric tubule. From these figures it is evident that the mesonephric tubule develops from a portion of mesoderm ventral to the pronephros; but according to both Rückert and van

[1] Figures 18 and 19, referred to by Wiedersheim ('90[b], p. 413) in this connection, do not relate to Reptiles at all. They represent sections of Duck embryos.

Wijhe, the mesoderm which produces the mesonephric tubules in Selachii belongs to a region dorsal to that which gave rise to the pronephros (see the diagrams appended to van Wijhe, '89, Taf. XXXII.).

In view of the difficulties to which I have alluded, it seems to me that Hoffmann's position cannot be regarded as satisfactory. Furthermore, if Hoffmann's observations[1] on the origin of the posterior mesonephric tubules be accurate, the contrast which Mihalkovics endeavored to establish between the anterior and posterior tubules does not exist. If, finally, these anterior three or four pairs of tubules develop in their course typical Malpighian capsules remote from the peritoneum, — Mihalkovics is not clear on this point, — I can see no reason for regarding them as pronephric. I am therefore of opinion that there is at present no evidence which *proves* a pronephros to exist either in Lacertilia or in Ophidia.

It remains for me to consider two recent papers by Wiedersheim ('90[a], '90[b]), which describe a very interesting condition of the excretory system in Crocodilia and Chelonia. The anterior portion of the embryonic excretory organs in these groups consists of a number of tubules which take their origin in ciliated nephrostomes, and, after undergoing contortion, join a longitudinal canal continuous with the segmental duct. From the root of the mesentery a large glomus protrudes into the body cavity. It lies in a distinct fold of the peritoneum, and consists of a mass of highly vascular tissue receiving distinct vessels from the aorta. It extends continuously opposite a number of nephrostomes, and is evidently equivalent to the Amphibian glomus. In somewhat more posterior regions the conditions are essentially the same; but the nephrostomes and the glomus having approached each other, they are cut off from the main portion of the body cavity by a longitudinal fold of peritoneum. In this manner, there is formed a pronephric chamber comparable to that of Amphibia. In yet more posterior regions, the pronephric chamber with its contained glomus breaks up into a series of capsules containing glomeruli, each of which then appears to form the blind termination of a tubule. This is the region of the mesonephros with typical Malpighian capsules. In the subsequent development of the embryo, the anterior portion of this excretory system early atrophies, and the hinder part alone constitutes the well known Wolffian body, or mesonephros. In my opinion, the account given by Wiedersheim affords a satisfactory basis for the view that the most anterior portion of this excretory system is truly pronephric. It seems, however, quite impos-

[1] Similar observations are recorded by Orr ('87, pp. 325–327).

sible to draw a rigid line between pronephros and mesonephros. Indeed, such is a part of the conclusion which I think we shall finally be able to draw from the entire review.

The numerous accounts which have been recently given of the pronephros in the higher Amniota may be conveniently treated under three heads : —

(1.) According to Balfour and Sedgwick ('78, '79), the Müllerian duct in the Chick first appears in a region somewhat behind the front end of the Wolffian duct as three slender invaginations of the peritoneum which covers the Wolffian body. These invaginations later fuse at their distal extremities, and the most posterior involution grows backwards in connection with the Müllerian duct. There is thus formed a longitudinal canal with three peritoneal funnels, the whole structure being comparable to the pronephros of Amphibia. Slightly in front of the nephrostomes there is attached to the radix mesenterii a vascular body which resembles the Amphibian glomus. It receives blood-vessels from the aorta, and projects into the body cavity enclosed in a distinct sac of peritoneum. Gasser ('74, pp. 58, 59) had previously observed somewhat similar conditions in the anterior end of the Müllerian duct; and, by renewed investigation, Gasser and Siemerling were able to confirm the occasional occurrence of the phenomenon, though a single invagination appeared to be the rule. Multiple invaginations have also been mentioned by Kollmann ('82[b], p. 20), Siemerling ('82, p. 29), Janošik ('85, p. 43), and Mihalkovics ('85, p. 295); but Braun ('79) and Renson ('83, p. 37) were unable to find any evidence of such a condition. Braun also opposed Balfour and Sedgwick in their view respecting the nature of the vascular body, and Sedgwick ('80[b]) later came to the conclusion that this structure was really a series of greatly modified mesonephric glomeruli. This interpretation was adopted by Balfour ('81[a], p. 590).

(2.) The second view is set forth in the recent account of Felix ('90), who describes in a chick embryo with eight protovertebræ a series of outgrowths, which, emerging from the lower hinder portions of protovertebræ IV.–VIII., extend backward and outward toward the ectoderm. The latter layer occasionally presents local thickenings in this region, and in some cases a connection between the mesodermal outgrowths and the ectodermal thickenings can be observed. In older embryos no trace of the structures can be found. As was the case with the evaginations found by Hoffmann ('89) in Reptiles, no fusion of their distal extremities is recorded. This condition makes them at once unlike the Selachian pronephros described by Rückert, and the early stages of the Amphibian

pronephros as detailed in the preceding pages. Moreover, Felix produces no evidence to show that they stand in any genetic relation whatever to the Wolffian duct, or to the pronephric structures described by other authors. In the present state of knowledge his interpretation seems to me untenable.

(3.) The remaining views all have the common feature that they regard certain rudimentary canals in connection with the anterior end of the Wolffian duct as pronephric. The views are somewhat divergent, but I have been able to compile from them a general statement which will in a measure explain their conflicts. In bringing the observations of each author under this general scheme, I shall frequently be driven to regard his results as incomplete, but I shall as far as possible avoid questioning his statements from an *a priori* standpoint.

In general three regions of the embryonic excretory organ may be distinguished: the pronephros, an intermediate region, and the mesonephros. For criteria of these regions, I shall use in the main glomerular structures: those of the pronephros are glomi wholly external to the tubules; those of the intermediate region are transitional glomeruli, which develop in peritoneal canals, but project through the nephrostomes into the body cavity; those of the mesonephros are typical glomeruli, which have only a mediate connection with the body cavity through the tubule.

It now remains to consider the results of the observers whom I have placed in my third group. The work of Gasser and Siemerling ('78, '79), subsequently carried on by Siemerling ('82), relates to Birds alone. These authors recognize two distinct portions of the Wolffian duct: a portion lying in front of the fifth somite, and a posterior portion. The former shows many irregularities, is broken up into discontinuous fragments, and early atrophies; the latter develops more slowly, but more regularly, and persists as the duct of the Wolffian body. The first indications of tubules consist of the so-called primary cords, which are continuous with the cœlomic epithelium by means of funnel-shaped ostia, while they are distally in contact with the duct. Gasser and Siemerling maintain that they belong to the most anterior part of the mesonephros, a portion which early atrophies. They are quite similar to the S-shaped canals of Kölliker ('79). In front of the region of the "primary cords" similar evaginations occur, but these never reach the duct. A typical glomus, which may be single or may be divided into parts, projects from the radix mesenterii opposite the openings of these evaginations. In embryos of this stage the space between the most anterior Wolffian tubule and

the pronephric structures is traversed by a series of glomeruli which resemble most closely those of the mesonephros. Siemerling calls them transitional glomeruli. The pronephros of our scheme would be represented in this account by the region in front of the fifth protovertebra; the intermediate region would correspond to the space occupied by the transitional glomeruli, and also, as I believe, to that previously occupied by the primary cords; the mesonephros would form the rest of the organ.

According to Sedgwick's ('81) account of the development in the chick, the Wolffian duct, in separating from the proliferation in which it arises (region between the 7th and 11th protovertebræ), remains connected with the peritoneal epithelium by short cords of cells. Between the 8th and 15th protovertebræ, the duct, as it grows freely backwards, comes secondarily into contact with such a cord of cells in each somite. Behind the 15th somite, the fundaments of the tubules (intermediate cell mass) do not join the duct until their differentiation is somewhat advanced. The cords of cells in the region between the 7th and 11th protovertebræ acquire lumens which may be continued even into the duct; but both cords and duct soon entirely disappear. Although no glomus is described, this region probably represents the pronephros. Between the 12th and 15th protovertebræ typical nephrostomal funnels are formed, in which transitional glomeruli develop. This portion of the organ would then correspond to the intermediate region of the general scheme; behind this region comes the typical mesonephros. Sedgwick regarded the first mentioned region as pronephric; but he hoped to be able to harmonize such a view with the position (*cf.* page 276) formerly taken by himself and Balfour (Balfour and Sedgwick, '79).[1]

In the foregoing description I have assumed that the most anterior portion of the Wolffian duct and the accompanying transverse canals observed by Sedgwick corresponded to the pronephric region as described by Siemerling. This interpretation seems to me in all probability correct; yet it should be recalled that the pronephros described by Siemerling lies in front of the 5th somite, and is anterior to the region in which the early proliferation to form the duct took place; whereas,

[1] Mihalkovics's statement, that Sedgwick abandoned his former view, is incorrect, as will be seen by referring to the closing paragraph of his article (Sedgwick, '81, p. 468).

In the second edition of Foster and Balfour's ('83, p. 218) Elements of Embryology, revised by Sedgwick and Heape, the anterior end of the Müllerian duct is the only homologue of the Amphibian pronephros suggested.

the pronephros, according to Sedgwick, lies between the 7th and 11th protovertebræ and arises in the same region in which the duct first appears.

Lockwood ('87, pp. 657–663) describes three regions in the embryonic excretory organ of the Rabbit. In the most anterior region (pronephros), the duct consists of isolated fragments, which are connected with the body cavity by 2–3 nephrostomes. Then follows a region of typical nephrostomal canals with glomeruli, and finally typical blind mesonephric tubules. Possibly the last two regions belong to the mesonephros; but in none of the accounts of Mammalian development have I been able to recognize with certainty the intermediate region.

According to Renson ('83, p. 29), glomeruli develop in the Chick in the region of the pronephros, which is otherwise described in agreement with Sedgwick's account. The pronephric tubules atrophy with the exception of their nephrostomes, and in the hollow of each funnel there appears a glomerulus which soon comes to project freely into the body cavity. In a region directly posterior to that in which the free glomeruli occur, there are found the so-called mixed glomeruli, which are situated in the base of an infundibular depression, and are partially covered by a fold of peritoneum. This, as well as the more anterior portion of the system, Renson regards as belonging to the pronephros. He also describes in the Rabbit a series of peritoneal involutions in connection with a discontinuous duct. In this region he likewise observed a vascular structure, which he regarded as a very rudimentary external glomerulus. A similar observation has been recorded for human embryos by Lockwood ('87, pp. 662, 663), and for Arvicola by Spoof ('83, p. 86, footnote). It is difficult to arrive at a satisfactory estimate of Renson's position. There would be no difficulty in classing him with Sedgwick, were it not for the circumstance that he describes for the pronephric region (6 or 7th to 11 or 12th somites) glomerular structures which, according to his own comparison, develop in the same way as the transitional glomeruli observed by Sedgwick in the "intermediate" region only (11th to 14th somite). If, however, it should prove to be true that only the "mixed" glomeruli develop in this way, the conflict would at once be removed, and Renson's account would show the three primary regions in their typical condition.

According to Mihalkovics the most anterior two or three tubules (1–7 somites) in the Chick and Duck are derivatives of the communicating canals, and gain a connection with the duct while yet opening into the body cavity by a distinct ostium. The posterior canals, on the contrary,

are all differentiated from the solid "Wolffian blastema," and never have any connection with the body cavity. Posterior to the last pronephric canal, 5–6 free glomeruli are to be found. The anterior canals form much earlier than the posterior, indeed they wholly abort before the mesonephros attains its final development; and they together with the free glomeruli are, in his opinion, to be regarded as equivalent to the pronephros and glomus of Amphibia. Mihalkovics also mentions the occurrence of transitional glomeruli; these are typical glomeruli which lie near the peritoneal covering of the Wolffian body. It seems to me probable that these glomeruli really belong to the mesonephros, and that at least a portion of the "external glomeruli" belong in reality to the class which I have designated transitional glomeruli. This interpretation would not merely be in agreement with the described position of the glomeruli with reference to the somites, but it would also accord well with the figures Mihalkovics gives of the two sets of glomeruli. Thus, in his representation of a transitional glomerulus (Taf. I. Fig. 17, *g. m.*), there is little reason to regard the structure as in any way different from a mesonephric Malpighian body. I may here further remark, that nearly all other modern investigators agree in deriving a part, if not all, of the mesonephros from a layer of cells which primitively bounded the cœlom, rather than from a strictly indifferent blastema. In this light, the validity of the principal contrast Mihalkovics sought to establish between the pronephros and mesonephros becomes at least very uncertain.

The account of Janošik ('85) affords the best basis for the general scheme I have proposed. The most anterior region, or pronephros, develops somewhat *later* [!] than the first tubules of the mesonephros (primary cords?). The duct in the region of the pronephros is broken up into fragments, which receive rudimentary peritoneal canals. Three typical glomi are developed on the radix mesenterii. In the next following region (intermediate), from two to five peritoneal canals communicate with the Wolffian duct. Near the nephrostomal ends of these canals transitional glomeruli develop. Both the pronephros and the intermediate region rapidly atrophy. The remaining portion of the embryonic excretory organ is the true mesonephros. The mesonephric tubules are either developed as separate buds from the peritoneum, or are differentiated from a blastema which is directly derived from the peritoneum. Janošik was able to confirm Renson's discovery of rudimentary pronephric tubules in the Rabbit, but was unable to find in this form any trace of external glomeruli. Later, however, he ('87, p. 582) described in a young human embryo, 3 mm. in length, a peculiar projection into the

body cavity. The structure resembled the external glomerulus of Birds, and he was inclined to interpret it as such in this case.

In the preceding pages I have endeavored to present a comprehensive résumé of the development of the pronephros as described in groups of Vertebrates other than Amphibia. In this review it has been shown that an equivalent of the Amphibian pronephros has been claimed to exist in all Craniota; and that a mode of development similar to that described in the early part of the present paper has been found in Selachii by Rückert ('88) and van Wijhe ('89), in Petromyzon by Kupffer ('88), and in Lepidosteus by Beard ('89). The Reptilian pronephros as described by Hoffmann ('89), and that of the Chick according to the account of Felix ('90), do not seem to me to be in perfect accord with this mode of development.

It now remains for me to compare the results of my studies, as detailed in the descriptive part of the present paper, with those which have been recorded by other writers on the development of the Amphibian pronephros. According to the account which at present receives most general acceptance, the pronephros first appears as an outfolding of the somatopleure in the form of a longitudinal groove. The anterior end of this groove is destined to become the pronephros; the remaining portion is constricted off to form the segmental duct. Since the process of constriction advances from before backwards, stages may be found in which a completed tube is continuous posteriorly with a mere groove of the somatopleure. In the anterior region, the groove remains in communication with the body cavity, and grows down towards the ventral surface of the embryo in the form of a broad pocket. The slit-like peritoneal opening of this pouch closes throughout the greater part of its length, leaving, however, two or three regions of incomplete closure, the fundaments of the nephrostomes. The nephrostomal tubules are formed by the fusion of the walls of the pouch between two nephrostomes. The regions of fusion extend in vertical lines from the nephrostomal margin of the pouch nearly to its ventral border, where there is left an unfused and therefore continuous longitudinal tract constituting the canal which I have called the collecting trunk. This view of the development of the pronephros, although suggested by Wilh. Müller ('75), was first described in detail by Goette ('75) for Bombinator, and was later extended to other Amphibia by the researches of Furbringer ('77). It has been entirely confirmed by Wichmann ('84), by Hoffmann ('86), and still more recently by Marshall and Bles ('90[a]).

In opposition to this view, I would maintain: (1) that the first trace of the excretory system consists of a solid proliferation of somatopleure, the pronephric thickening; (2) that the lumen of the system arises secondarily; and (3) that the pronephric tubules do not appear in consequence of the local fusion of the walls of a widely open pouch, but that they are differentiated at an early stage from the hitherto indifferent pronephric thickening.[1]

The development of the pronephros and duct from a solid mass of mesoderm was a common feature in the accounts of those who wrote prior to Wilh. Müller and Goette, but since then this mode of origin, though repeatedly maintained by single observers, has failed to gain general acceptance. Clarke ('81) described a solid pronephric thickening, and asserted that the lumen arose secondarily in this mass; the details of the process are, however, not accurately given. Duval ('82) also described the pronephros as first appearing in the form of a solid thickening. He however states that it later acquires a slit-like opening into the body cavity, and that by the imperfect closure of this opening the successive nephrostomes are formed, as described by Goette and Fürbringer. This latter statement I am unable to confirm. Gasser's ('82, pp. 89–97) short note gives, on the other hand, an account of the early development in Alytes, which is in substantial agreement with my own observations. His account of the first differentiation of the nephrostomal canals is not very full, but it is not improbable that he conceived it to take place in a manner altogether similar to that which I have described. His statements seem to me in general correct,[2] but incomplete.

Janošik ('85, p. 19) states, on the basis of personal observations, that the first trace of the segmental duct in Bufo and Triton is a solid mass of cells, which he is, however, inclined to regard as a disguised fold of somatopleure.

According to a recent account by Kellogg ('90), a lumen does not appear anywhere in the organ (except in the region of the nephrostomes) until it has been separated from the peritoneum. Finally, Mollier ('90, Rückert and Mollier, '89) has published an account of the early development, which is for the most part in close accord with the results of my own studies. Since these results were gained entirely independently of

[1] The large cavity which the pronephric pouch presents in Stage IV. of Rana and Bufo is a secondary condition produced by the expansion of the lumens of the several diverticula.

[2] I must here except his statement that the second tubule is differentiated before the rest; this I believe to be an error.

Mollier's researches and were written out before his paper came into my hands, it seems to me that my confirmation of his position affords excellent evidence of the correctness of the view advocated. In one feature alone our accounts of the earliest condition of the pronephros would seem to differ widely, but I am confident that the difference is apparent rather than real. Mollier states that each of the diverticula which form the first indications of the nephrostomal canals emerges from a protovertebral cavity. This statement, as I have already shown, does not in my opinion accurately represent the actual conditions. In the stage under consideration, the dorsal portion of the mesoderm is in the anterior region divided by transverse planes into a series of metameric blocks; the pronephric thickening also is made up of metameric constituents, and is continuous dorsally in Amblystoma with two, in Rana and Bufo with three, of the blocks of mesoderm. As yet no definite line can be drawn between the protovertebræ and the lateral plates; in a slightly older embryo, however, the protovertebræ begin to be constricted off from the lateral plates, and it is at once evident that the pronephric tubules have to do with the ventral segment of the mesoderm. This difference in our accounts seems to me then very trivial, and my only excuse for dwelling upon it is the circumstance that Rückert and Mollier seem to attach great morphological significance to this feature of their account. This relation to the protovertebræ seems to me quite untenable.

Previous authors have been singularly reticent respecting the exact position of the pronephros with reference to the body somites. Fürbringer ('78[a], p. 5) states that the pronephros of Anura extends over three, that of Urodela over two somites; but I have looked in vain for a statement which should show whether the nephrostomes are segmental or intersegmental in position. Kellogg states that each nephrostome occurs opposite the middle of a protovertebræ. Marshall and Bles confirm this statement, and contend that, in the case of Rana, the nephrostomes lie in the 2d, 3d, and 4th somites behind the auditory vesicle. According to Mollier ('90, p. 213) the pronephros appears in Triton in the region of the 1st and 2d trunk protovertebræ; but since the most anterior two protovertebræ are reckoned to the posterior region of the head, these represent the 3d and 4th protovertebræ of the series. The enumeration which I have given for Rana and Bufo is in precise agreement with that of Marshall and Bles. For Amblystoma my account is in agreement with that of Mollier for Triton.

I am not aware that any definite attempt has thus far been made to ascertain which of the three nephrostomes of Anura is unrepresented in

Urodela. At first sight it would seem probable, — and by implication I accredit this opinion to Mollier, — that the rudimentary third tubule occasionally present in Urodeles corresponds to the normal third tubule of Anura. This view, however, is not in precise harmony with the relations of the nephrostomes to the myotomes. As I have already shown, the first nephrostome in Amblystoma is situated beneath myotome III., whereas in Rana and Bufo it occurs under myotome II. If now the enumeration of the somites in the two cases correspond, it follows that the first and second nephrostomal tubules of Amblystoma are equivalent to the second and third tubules respectively of Rana and Bufo, not to their first and second tubules, and that the occasional rudimentary third tubule of Urodeles belongs to a more posterior somite, and is unrepresented in Anura. In Amblystoma the root of the vagus nerve arises immediately in front of the somite which I have denominated I.;[1] the same is true in the case of Rana and Bufo, and I am inclined to regard these as equivalent somites. It is possible that somite II. of Amblystoma is not represented in Rana and Bufo; but this is hardly probable, since it belongs to the head region, which is hardly likely to vary in such closely related groups, and since it is evident that the greater number of protovertebræ present in Urodeles as compared with Anura is largely accounted for by additional protovertebræ in posterior regions, particularly in the region of the mesonephros, as I believe. In general, it seems to me that we should be more ready to admit the abortion of the most anterior tubule in Urodela than to assert the existence of an additional protovertebra in Anura.

All the more recent writers are agreed that in Anura three pairs of pronephric nephrostomes occur, Giles ('88, p. 135) alone claiming that a degenerating pronephros may have four. In Urodela the typical number is two; but Mollier ('90, p. 224) has recorded the occasional occurrence of three pairs in Triton, and I have made similar observations in Amblystoma. Spengel ('76, p. 19, Taf. II. Fig. 21) maintained, on the evidence of a specimen in which the pronephros was largely degenerated, that four pairs occur in Cœcilia; the recent observations of Semon ('90, p. 462), on the other hand, have shown that there exist in Ichthyophis on *each* side of the body ten *pairs* of nephrostomes, therefore forty in all.

[1] Somite I. of this enumeration probably corresponds to the one which has been called somite XI by Houssay ('91). Houssay believes that he can identify in Amphibia the somites which have been observed in the head region of Selachii. If his conclusions are accurate, they are evidence in favor of the view that this region of the body is very permanent.

Of the two nephrostomes belonging to any pair, one opens freely into the body cavity, the other communicates with a pronephric chamber, which contains the glomus and is completely shut off from the body cavity. The meaning of this condition I shall consider in the subsequent discussion. The pairs of nephrostomes on each side are slightly more numerous than the overlying protovertebræ.

The origin of the so-called ventral part (common trunk) of the pronephros has recently become the subject of controversy. According to Goette the duct at first communicates with the posterior end of the widely open pronephric pouch. At the same time that the nephrostomal canals are formed by local fusions of the walls of the pouch, a similar process constricts off the posterior ventral portion of the pouch; this has the effect of lengthening the duct, so that the point of its attachment is carried forward to the place where the converging nephrostomal tubes unite. The portion of the longitudinal canal in front of the most posterior nephrostome represents the "ventral part" of the pronephros.

According to Fürbringer, the longitudinal groove which forms the earliest fundament of the pronephros and duct becomes entirely constricted off from the somatopleure as far forward as the opening which leads into the pronephric pouch; this slit-like opening then elongates posteriorly, so as to extend into the region formerly occupied by the longitudinal canal alone; the latter thus comes to lie ventral to the last nephrostomal canal, and forms the ventral part of the pronephros.

Kellogg ('90) opposes the accounts of previous observers, and claims that the ventral part "is formed from the ventral side of the dorsal part of the pronephros, and *anterior to the last nephrostome*." Marshall and Bles, alluding to Kellogg's description, declare that it is in exact accordance with the accounts of Goette and Fürbringer. I have not been able to satisfy myself as to the precise manner by which Kellogg conceives the formation of the ventral part to have taken place; but I think he has said enough to contrast his position strongly with that of Fürbringer, according to whom the ventral part of the pronephros first appears as a portion of the somatopleural fold immediately *posterior* to the part which gives rise to the nephrostomal canals. Kellogg argues, however, that, were the views of previous authors correct, some portion of the pronephros would appear behind the last nephrostome; but this is actually never the case. The force of this argument I am wholly unable to appreciate, and I must in consequence feel some doubt as to whether I have properly interpreted Kellogg's previous statements.

According to Mollier, the "ventral part" is differentiated in the

ventral portion of the broad pronephric thickening. Mollier's description is substantially in accord with my own observations, and it seems to me probable that Kellogg's statements are to be understood in the same way.

The structure of the functional pronephros was early the occasion of much controversy. The discoverer of the organ, Joh. Müller ('29 and '30), describes and figures it as a cluster of blind tubules, which radiate in the form of a rosette from the anterior tip of the segmental duct. This view was shared by the larger number of the early investigators. According to von Wittich ('52), the gland is typically formed by the convolutions of a single tube; in the more complicated pronephridia, however, this canal may give off branches. It is to Goette and Fürbringer that we owe the first accurate account of the process of convolution.

According to these authors, the gland is composed of two portions: a "dorsal part" (collecting trunk and nephrostomal canals), which alone receives the nephrostomes,[1] and a "ventral part" (common trunk), which serves as the efferent canal, and is in communication with the anterior end of the segmental duct. Both ventral and dorsal parts undergo extensive convolutions, and give rise to blind diverticula. Subsequent authors have in general confirmed Fürbringer's account, but have added no new matter to the description. Selenka ('82) describes and figures an interesting condition of the pronephros in Hylodes. The glands of the two sides are unsymmetrical, and depart widely from the typical structure known in Amphibia. Following the nomenclature which I have proposed in the descriptive part of this paper, it is evident that the nephrostomal canals and the collecting trunk are present, but do not show the convolutions customary in these parts. The "ventral part" of the gland, however, is not formed by the windings of the common trunk, but is composed of great irregular blind pouches which communicate with the collecting trunk, while the latter opens *directly* into the anterior end of the segmental duct. This condition of the pronephros evidently represents the degeneration of the gland, and Selenka is inclined to correlate the premature appearance of this complication in Hylodes with the absence of gills in the larvæ of this form.

Kellogg has studied the structure of the pronephros in Amblystoma and Rana by means of reconstruction from cross sections. His pre-

[1] Duval ('82, Fig. 7), figures the second pronephric nephrostome in Rana as opening directly into the ventral part of the gland. I have never seen such a condition in my preparations, nor do I know of similar observations being elsewhere recorded. It seems likely that Duval has here fallen into error.

liminary notice, however, does not describe the process of convolution in detail. An interesting feature is the statement that blind diverticula do not appear until the tubes of the gland have become very much convoluted. In the pronephridia which I have studied, I have never seen a blind diverticulum. My observations do not extend to sufficiently old stages to allow me to deny that such diverticula appear anywhere in the developmental history of the gland, but the organ can reach at least the high degree of complexity shown in Figures 41 and 65, and yet be composed of the windings of the nephrostomal canals, the collecting trunk, and the common trunk without possessing any blind diverticula.

It is needless for me to discuss in this place the histology of the tubular portion of the pronephros. These details have little general interest, and they have furthermore been accurately given by Fürbringer and Hoffmann ('86).

The dilated chamber which I have described (page 240) was also observed by Hoffmann, but he was unable to determine what portion of the system was concerned in its formation. Similar dilated chambers are likewise described by Marshall and Bles, who regard them as steps in the degeneration of the tubules. The early appearance of these dilated regions in Rana (see page 232) seems to me to render this interpretation improbable.

According to the usual account, the capsule arises as a differentiation of the connective-tissue stroma, which lies between the pronephros and the ectoderm. Duval ('82, pp. 25, 27) alone has claimed an origin from the overlying protovertebræ; but, singularly, his statement has been wholly neglected by subsequent writers. His observations on this point agree in all essential features with my own.

The glomus was discovered by Joh. Müller ('30, p. 12), but the significance of the structure was wholly problematical until Bidder ('46, p. 58) suggested its glomerular nature, which has since received general acceptance. This view has, however, been opposed by Semper ('75, pp. 439 *et seq.*), and more recently by Hoffmann ('86, pp. 572, 573). According to Goette and Fürbringer, the glomus arises as an outfolding of the splanchnopleure opposite the pronephric nephrostomes. The interior of the fold becomes occupied by mesenchymatic cells and with blood tracts, which communicate with the aorta. According to Hoffmann, the interior is largely occupied by "columns" of large cells, which would seem foreign to the nature of a glomerular structure. These 'columns of cells," he says, may be seen to arise, in Bufo at least, by the invagination of the superficial covering of the glomus. I have myself seen continuous cylin-

drical cords of cells in the glomus; but in most cases I have been readily able to satisfy myself that this appearance had to do with densely packed blood cells lying in a definite vascular tract. I have also occasionally met with invaginations of the superficial (peritoneal) epithelium of the glomus (page 247); but it seems to me, even should it be shown that they give rise in the interior to columns of cells, that this would not be a very serious objection to the view which ascribes to the organ a glomerular function. In favor of that view, many arguments may be adduced: (1) the highly vascular nature of the glomus; (2) its position in an open chamber of the body cavity directly opposite the pronephric nephrostomes; (3) its serial relations with the mesonephric glomeruli; (4) its appearance and degeneration synchronously with the pronephros; and (5) the circumstance that its homologue, wherever found in other classes of Vertebrates, is always in equally close relation with excretory tubules. The last argument seems to me the most weighty, and I am of opinion that a comprehensive comparative study proves beyond question the glomerular nature of the structure.

In the descriptive part of this paper I have stated that, in satisfactory sections through the blood-vessel which leads from the aorta to the glomus, one could frequently observe that the ramifications within the glomus did not appear to be terminal, but that the vessel seemed to give off a lateral branch to the glomus, while the main trunk continued on toward the ventral side of the body. An explanation of this condition has occurred to me, which, if confirmed, will be of considerable morphological significance, though at present I can merely offer it as a suggestion. As we have already seen, the glomus of Selachii, according to Rückert ('88, pp. 239–242), does not receive a separate blood-vessel directly from the aorta, but a rete mirabile is developed in connection with the segmental vessels described by Paul Mayer. I have not succeeded in tracing the main aortic branch to the ventral side of the larva; but, as far as it could be followed, the course of the vessel between splanchnopleure and entoderm corresponds perfectly with that of one of the segmental vessels described by him. It seems to me quite possible that, in Amphibia, the dorsal portion, which is in communication with the glomus, is the only part of these rudimentary vessels which is retained, and that the remaining portion, having ceased to be of functional importance, fails to develop.

Having completed my survey of our knowledge of the development of the pronephros in the several classes of Vertebrates, I now turn to a

consideration of the development of the segmental duct. As is well known, observers up to a very recent date have been almost unanimous in ascribing a mesodermal origin to this structure. In regard to the details of the process, however, they have been less at one; and I shall accordingly treat of their accounts under three heads, which seem to me to represent fairly well marked phases of opinion.

According to one view, *the duct arises as an evagination of somatopleure, its lumen being therefore a detached portion of the body cavity.* Such a mode of origin was advocated by Rosenberg ('67, pp. 42 *et seq.*) for Teleosts; and this feature of his account has gained almost universal acceptance both for Teleosts and for Amphibia, having been recently entirely confirmed by Hoffmann ('86) and Henneguy ('88, '89). According to Wilh. Müller ('75) and Fürbringer, the duct arises in this way also in Petromyzon, and a similar claim has been made for Ganoids by Kowalewsky, Owsjannikow, and Wagner ('70), and by Balfour and Parker ('82). In Selachians, however, the weight of the evidence is distinctly opposed to this view, and I am not aware of its having been advocated by any one besides Schultz ('75).

In Amniotes also such an account of the early development has not received general acceptance; it was first claimed in this class by Romiti ('74), and was adopted, with some modification it is true, by R. Kowalewsky ('75), and by Dansky und Kostenitsch ('80, p. 24). Very recently such a mode of origin has been reasserted by Fleischmann ('87) for Carnivores and the Duck.

My own observations on Amphibia indicate that in this group the duct does not arise as a fold; and I am of opinion that, in both Cyclostomes and Ganoids, the evidence that the duct arises by evagination is at present unsatisfactory. It seems to me probable, on the contrary, that the method of origin which is usually recognized as characteristic of all the Anamnia with the exception of Selachii exists, if at all, only in Teleosts. In view of the peculiar obstacles which Teleostean material presents for embryological study, one should be cautious in affirming for this group a mode of development which, in my opinion, is not proved to exist in any other class of Vertebrates.

A second view of the origin of the duct is, that it *arises from a solid proliferation of somatopleure.* According to Fürbringer ('78[a]), Spoof ('83, p. 84), and the earlier writers (Remak, '55, Kölliker, '61, Bornhaupt, '67, Waldeyer, '70, and Foster and Balfour, '74), the duct arises in the chick by a proliferation *in situ* of the subjacent mesoderm, and a similar origin is maintained for Petromyzon by Scott ('82). The more recent

view, however, affirms that the posterior end of the duct grows backward free from adjacent tissue, the cellular material being wholly derived from an anterior proliferation. For Selachii this method of origin has been maintained by Balfour ('78), and for Amniotes by a large number of observers; e. g. Weldon ('83) and Mihalkovics ('85) in Reptiles; Gasser ('77), Sedgwick ('81), Schmiegelow ('81 and '82), and Janošik ('85), in Birds; Renson ('83) and Martin ('88), in Mammals. Gasser ('82) believes that the segmental duct in Alytes has no direct connection with the mesoderm, posterior to the pronephros; but he was unable to exclude with certainty the possibility that the somatopleure immediately behind the pronephros might take some part in the formation of the duct. Mollier ('90, p. 226) moreover asserts that such a participation actually takes place in the two somites following those in which the pronephros is formed, but that the posterior portion of the duct probably grows back from this point independently of the mesoderm.

In so far as these authors maintain that the duct arises from a solid proliferation of mesoderm and acquires its lumen secondarily, I entirely agree with them; but my observations on this point lead me to conclude further that the duct arises throughout its entire length from a continuous thickening of somatopleure, and that the only free growth which occurs in the Amphibia studied by me is for the purpose of effecting a union with the cloaca. In assuming this position, I am aware of being in conflict with prior observations on Amphibia, and with the more recent accounts of the development in other groups; it seems to me, however, that satisfactory evidence in favor of this mode of origin has been adduced in the descriptive part of this paper.

Finally it remains for me to consider the third view, that of the ectodermal origin of the duct, which is to-day advocated on so many sides. As early as 1855 Remak expressed himself as dissatisfied with the derivation of the excretory system from the mesoderm, although this mode of origin was confirmed by his own observations. A decennium later His ('65[b], pp. 160–162) maintained that, in the Chick, the Wolffian and Müllerian ducts both arise as folds of the ectoderm; but he abandoned this position later ('68, p. 119), when it had been shown by Bornhaupt ('67) and Dursy ('67) to be untenable. He then endeavored to interpret the facts in harmony with his theoretical conceptions by maintaining that the cells from which the Wolffian and Müllerian ducts arose were primarily derived from the ectoderm, a view which was likewise adopted by Waldeyer ('70). Meantime Hensen ('66) had indorsed the view of a direct origin from the ectoderm. He states ('66, p. 81, foot-note) that

in the Rabbit the Wolffian duct arises from a solid rod-like thickening of the ectoderm near the middle protovertebræ. In a second short communication ('67, p. 502), Hensen merely reaffirmed his confirmation of His; but finally he ('75–'76, pp. 369–372) published a fuller account of his observations, accompanied with figures. These, however, are far from conclusive, and it does not seem surprising that this single observation was distrusted by subsequent writers.

In 1884 Graf Spee published an account of his very careful investigation of the subject, and reasserted the ectodermal origin of the Wolffian duct.[1] Following this publication have appeared a large number of confirmatory papers, which have moreover extended the observations of Graf Spee; so that at present the ectodermal origin of the duct has been asserted for every class of Vertebrates, with the single exception of the little known Dipnoi.

As stated in the Introduction to the present paper, it was my hope in undertaking these studies to find in Amphibia results confirmatory of Graf Spee's position. If, then, a contrary result has been reached, it has been because I have been driven to that conclusion by evidence brought out in the course of the investigation. In my opinion, the entire excretory system of the forms I have studied unquestionably develops without any participation of the ectoderm in its formation. The duct develops from mesoderm throughout its entire length, and at its posterior end, in Rana and Bufo at least, comes in contact with one of the entodermal cornua of the hind gut; so that *nowhere* in its development does it come into organic union with the outer germ layer.

I must in this case distinctly disavow the suggestion of Hertwig ('88, p. 280), who endeavors to harmonize the accounts by assuming that only the posterior end of the duct is formed from the ectoderm. This explanation would by no means be admissible, unless it be granted that the ectodermal constituent might in this case be reduced to nothing at all. On the other hand, it must be confessed that a fundamental opposition in the mode of development of an organ in two closely related groups is at present hardly reconcilable with our general conceptions of embryological processes.

[1] Graf Spee, and subsequently Flemming ('86), did not clearly recognize the fact that the Wolffian duct and the mesonephros develop in different ways, and were led to defend an ectodermal origin for the *excretory system*. This interpretation is in evident opposition to the accounts of others, and, in my opinion, is not justified by their own observation, even should these prove to be accurate in every particular.

It will therefore be of interest to review critically the most recent accounts in the several groups, for the purpose of ascertaining whether the ectodermal origin of the segmental duct be in any case actually demonstrated. For this purpose, only those papers which have appeared since Graf Spee's researches need concern us. Of these, the larger number are brief notices, which, in view of the extreme difficulty of the investigation, cannot be regarded as conclusive.

In regard to Cyclostomes, the only papers that have appeared during this period have been preliminary notices; that of Kupffer ('88) maintains an ectodermal, those of Goette ('88) and Owsjannikow ('89) a mesodermal, origin for the duct.

In Teleosts, the duct has been claimed to be ectodermal by Brook ('87) and Ryder ('87); but on the basis of my own observations, which are as yet incomplete, I am led to doubt the correctness of this claim, which has already been opposed by the observations of Henneguy ('88), of H. V. Wilson ('90), and of McIntosh and Prince ('88). In the account by Brook, it seems to me probable that the ectodermal thickening observed has in reality a very different significance (lateral line proliferation) from that attributed to it, an opinion which is shared by Wilson ('90, p. 58). The only recent paper dealing with the development of the Ganoidean excretory system is the preliminary notice of Beard ('89) on Lepidosteus. According to Beard, the duct is ectodermal.

In Amphibia, also, an ectodermal origin of the segmental duct has been asserted by Perenyi ('87) and by Brook ('87). Their communications, however, are both short notices, and in the absence of the final papers cannot be regarded as satisfactory evidence. Moreover, the mesodermal origin of the duct has been reaffirmed by Mollier ('90), Kellogg ('90), and Marshall and Bles ('90).

It is rather remarkable, that, in all the preceding classes, nothing but preliminary notices have ever appeared in favor of the ectodermal view. The same is true of Birds, where this mode of origin has been claimed as probable by Beard ('87) and by Brook ('87). On the other hand, a number of observers have carefully investigated the chick with this special purpose in view, and have been unable to find any evidence of a participation of the ectoderm in the formation of the Wolffian duct. Among these may be mentioned Janošik ('85), Mihalkovics ('85), and Hoffmann ('89). Peculiarly significant, however, is the fact that Graf Spee ('86) was unable with the use of the most various reagents to see any direct evidence of a genetic connection between the ectoderm and the Wolffian duct in the *Chick*.

In Reptiles, a number of writers have asserted that the Wolffian duct arises from the ectoderm. According to Perenyi ('87, '88, '89), irregular groups of cells are at an early stage budded off from the ectoderm covering the middle plate, and on the first formation of the segmental vesicles they form the cord of cells which has been recognized by prior writers as the fundament of the duct. In my opinion, no conclusive evidence is adduced to prove that the cells figured in the latter position ('89, Fig. 5, *ceW.*) are descendants of those which at an early stage form part of the ectodermal thickening. Mitsukuri ('88) and Orr ('87) have published short notes claiming an ectodermal origin for the duct; and, finally, Ostroumoff ('88[a], '88[b]) asserts that it is derived from the ectoderm in Phrynocephalus. It seems to me, however, that Ostroumoff's observations are incomplete at a critical point, and that no satisfactory evidence is brought forward to show that the ectodermal thickenings which he describes and figures ('88[b], Tab. III. Fig. 56) with all desirable clearness, are unquestionably the fundament of the Wolffian duct. They may be merely chance thickenings over the intersegmental depressions in the underlying mesoderm. On the other hand, Mihalkovics ('85), Strahl ('86), and Hoffmann ('89) have all sought in vain to find satisfactory evidence of a participation of the ectoderm in the formation of the Wolffian duct.

With all the preceding classes of Vertebrates, I am of opinion that the weight of evidence is at present in favor of the view that the excretory system is wholly derived from the mesoderm. For the remaining groups, Mammals and Selachians, however, no such claim can be sustained. The researches of Graf Spee on Cavia showed conclusively that a cord of cells representing the fundament of the Wolffian duct is continuous posteriorly with a ridge of tissue which is still in intimate union with the superficial ectoderm, and that, in the further development, a continuous cord of cells separates off from this ridge by the progressive formation of a split between the deep portion of the ridge and the superficial ectoderm. At first, a distinct membrana prima is reflected from the unmodified ectoderm over the ridge, and the partially separated fundament of the duct may still be in connection with the superficial ectoderm by means of such a membrane. This latter feature is also dwelt upon by Flemming ('86), who furthermore emphasizes the circumstance that in the ridge which forms the first rudiment of the Wolffian duct mitoses are especially abundant, and that the nuclear spindles are frequently perpendicular to the surface, i. e. are so situated that the ensuing cell divisions would tend to thicken the layer. The

general results of these two investigators have been confirmed by Bonnet ('87 and '88) in the Dog and Sheep, and a number of former advocates of a mesodermal origin have satisfied themselves of the correctness of the opposed view by a study of the preparations of these authors; e. g. His (see Spee, '84, p. 93), Waldeyer (see Janošik, '85, p. 13), and Mihalkovics (see van Wijhe, '89, p. 501).

The most recent paper on this subject is that of H. Meyer ('90), who claims an ectodermal origin for the Wolffian duct in man. The embryo upon which these observations were made was obtained by artificial abortion, and was at once preserved by histological methods; so that, in the opinion of the author, it would be unfair to ascribe his results to imperfect preservation, which so frequently renders observations on human material untrustworthy. On the other hand, the mode in which the duct is here claimed to originate, viz. as a conspicuous *fold* of ectoderm, is so different from the method of origin described in other Mammals that one cannot regard this observation based on a single specimen as conclusive evidence.[1]

A few recent writers have reasserted the mesodermal origin of the Wolffian duct even in the case of Mammals. Lockwood ('87, p. 642) criticises the evidence adduced by Graf Spee and Flemming, and compares their ectodermal ridge to a number of insignificant ectodermal thickenings which may be observed over depressions in the underlying tissue in diverse regions of the body. Lockwood entirely ignores the very definite relations which Graf Spee showed to exist at a certain stage between the fundament of the duct present in anterior regions and the continuous posterior ridge; his entire criticism therefore seems to me quite unwarranted. Fleischmann ('87) also reasserts in a preliminary note the mesodermal origin of the duct in Carnivora; but his description of the mode of origin is so entirely at variance with the accounts of recent authorities that his statements can hardly be regarded satisfactory before the evidence on which they are based is produced.

On the other hand, Martin (Stahl und Martin, '86, Martin, '88) accepts the main features of the development as described by Graf Spee and

[1] During the correction of these proof-sheets another paper has appeared which asserts a participation of the ectoderm in the formation of the duct in Man (Kollmann, '91). In the region of the middle plate there is found, according to this author, a close fold of ectoderm (Taf. III. Figs. 3, 4, *Anlage d. Urniere*, Fig. 8[a]) which he believes to be concerned in the formation of the duct, thus confirming Meyer's ('90) account. The later stages studied by Kollmann, however, are too far advanced to afford convincing evidence that his interpretation of the fate of this fold is accurate.

Flemming, but interprets their observations in a fundamentally different way. In the course of a painstaking investigation, in which more than forty series of sections were used, Martin never encountered conditions which in his opinion demonstrated a genetic connection of the duct with the ectoderm. He believes that the duct arises from a proliferation of mesoderm in the region between the 9th and 11th protovertebræ, and grows backward by cell division within its own mass. The posterior portion of the duct, however, fuses with the ectoderm so intimately that in certain regions it is quite impossible to recognize a boundary between them; but Martin believes that the fusion is wholly secondary, and that the ectoderm contributes no material to the duct. Keibel's ('88[a], p. 635) studies on Erinaceus led him at first to accept Martin's attempt at harmonizing the two views; but in Cavia ('88[b], pp. 424–428) his observations inclined him towards the original view of Graf Spee.

In my opinion, Martin is right in denying that an ectodermal origin of the Wolffian duct has been demonstrated in Mammals. It is undoubtedly true, that there is considerable evidence in favor of such a mode of origin; but it is not of a nature that would warrant one in concluding that the duct arises in this way throughout all Vertebrates, or in asserting that it develops in fundamentally different ways in Mammals on the one hand, and in other Vertebrates on the other. All that can be claimed, however, in accordance with Martin's view, is that it is possible to interpret the conditions in Mammals in agreement with observations in other Vertebrates, should these be shown to be less ambiguous.

In Selachians, the evidence in favor of an ectodermal origin of the duct is perhaps even stronger than in Mammals. In the former group, besides the preliminary communications of van Wijhe ('86, '88[a]) and Beard ('87), there have appeared two extensive papers by Rückert ('88) and van Wijhe ('89), which seem to place the ectodermal origin of the segmental duct almost beyond question; and, so far as I am aware, no recent observer has expressed doubts upon this point. It nevertheless seems to me that, before accepting this result as final, we have yet to inquire whether Martin's interpretation of the condition in Mammals cannot be applied also in Selachii.

It might be objected, that the latter view offers no explanation for the intimate fusion which must be granted to exist between the posterior end of the segmental duct and the ectoderm; yet this argument cannot invalidate the general conclusion, since a number of cases of such a union of two epithelial structures in their growth have been recorded, where no genetic connection is believed to exist. Such a conception is in-

volved, for example, in the account — contested, it is true — given by Carius ('88) of the anterior growth of the chorda in the "Kopffortsatz" of Cavia, the chorda being in intimate fusion with the underlying entoderm; or, again, the backward growth of the Amniotic Müllerian duct in close connection both with the Wolffian duct and with the adjacent peritoneum, as described by a number of recent writers.

In conclusion, then, I am of opinion that the more primitive condition, and that shown by most Vertebrates, is the development of the segmental duct independent of connection with the ectoderm; but that in certain groups the duct enters into a secondary union with the ectoderm. The question whether the ectoderm here contributes material to the fundament of the duct can at present receive no more definite answer than that contained in the foregoing discussion.

It has frequently been asserted that the mesodermal origin of the kidneys is not in harmony with our conceptions of the derivatives of this germ layer. As early as 1855 Remak saw a fundamental opposition in the mode of development which he described for the excretory organs, and that familiar in the case of other glands. According to his view, which received very general acceptance, the kidney is a unique example of a gland whose secreting surfaces are not derived from one or other of the bounding germ layers, ectoderm and entoderm.

In my opinion, this view must now be considered inaccurate. It is doubtless true that glands are usually developed either from the ectoderm or from the entoderm; this circumstance may merely be due to their apparently being seldom needed on mesodermal surfaces. Certain special regions, however, seem to require glands. Such regions are the sexual conduits in which, besides those glands which have special functions, such as the deposition of the secondary egg membranes[1] (Ludwig), we should expect to find glands similar to those which are found in the course of other canals leading to the exterior, such, e. g., as the trachea. I shall disregard the glands which develop in the ampullæ of the vasa deferentia, since these are derived from the Wolffian duct and consequently *may* be of ectodermal origin in Mammals, and shall take as a specific example the genital tract of the human female. It seems very certain that in Amniotes the Müllerian duct develops entirely independently of the Wolffian duct, as an evagination of the peritoneal covering of the Wolffian body. Moreover, whether we accept the view of van Ackeren ('89), that the hymen marks the region of fusion between the fused Müllerian ducts and

[1] The albumen secretion of the Hen's oviduct is a familiar example. According to Giacosa ('72) the oviducal secretion in Rana is largely composed of mucin.

the sinus urogenitalis, or that of Nagel ('89), who claims that the vagina is a product of the sinus urogenitalis, the boundary between the two constituents being marked by the os externum uteri, it must in either case be granted that the entire genital tract from the ostia abdominales of the oviducts to the os externum is of mesodermal origin. This entire system is lined with a continuous columnar epithelium, which is continuous below with the stratified epithelium of the portio vaginalis. In its histological characters this membrane closely resembles a typical mucous membrane, and is subject to the characteristic disorders of this form of tissue, cancer and catarrh. The Fallopian tubes are believed to be without glands;[1] in the region of the fundus and corpus, however, are numerous long tubular cœcæ which have been called uterine glands. It has not been demonstrated, however, that these structures exercise a secretory function; and they may merely serve to regenerate the mucosa cast in menstruation. In the cervical region occur glands (glandulæ Nabothi, Schleimkrypten) which are much shorter than those in the body of the uterus. These cervical glands secrete a viscous fluid of the characteristic ropy consistency of mucus, which at periods mingles with the catamenial flow,[2] and, in certain stages of pregnancy, forms a complete plug in the cervical canal. This secretion forms a dense mass on addition of alcohol; it swells conspicuously when placed in water; it stains blue with hæmatoxylin, and pink with picro-carmin; and, finally, according to Overlach ('85) its formation is attended with the same fundamental changes in the protoplasm at the distal end of the secreting cell which are familiar in the case of ordinary mucous secretion.[3] It is almost certain that the cervical glands produce true mucus. Not merely, then, does the mesoderm give rise to glands, but *it produces glands of the same nature as those found in mucous passages of ectodermal origin.*

A second view was that formulated by His ('65[a]), according to which

[1] The vagina also is stated by Veith ('89) to be normally glandless.

[2] Of interest in this connection are the observations of Artemjeff ('89), who describes mucous corpuscles as a constituent element of normal lochia.

[3] Through the kindness of Dr. C. S. Minot, I have been able to try in addition a few simple chemical tests on the cervical secretions. The cervical plug from a uterus of three months' pregnancy examined by me, proved to be soluble in potassic, sodic, and calcic hydrates, and in sodic carbonate; it is precipitated by nitric acid, but redissolves in excess; in strong acetic acid, on the contrary, it appears not to redissolve. The substance gives the proteid reaction with nitric acid, but not that with cupric sulphate. It also gave the specific mucin stain with methylen blue recommended by Hoyer ('90).

the ectoderm and entoderm alone are capable of giving rise to epithelial tissues. This view, which was associated with the derivation of the urogenital tract from the ectoderm, was naturally revived by Graf Spee ('84). More recent evidence, however, shows that it is only the Wolffian duct in regard to which the question of an ectodermal origin remains open; the Wolffian tubules, on the other hand, as well as the epithelia of the female sexual tract, are distinctly mesodermal. The statement that epithelia do not arise from the mesoderm is, in my opinion, either insignificant or untrue. If, avoiding genetic characters, we define epithelium so narrowly as to exclude endothelium, we must confess that, except in certain specialized regions, epithelia do not develop from the mesoderm; but the conclusion is obviously of little morphological importance. On the other hand, if we employ broad morphological characters in our definition, such a conclusion is manifestly inaccurate.

The ectodermal origin of the Wolffian duct has been supposed to account for certain pathological new formations which frequently have their seat in the urogenital organs. Thus His ('65[b]) saw in the mode of development which he described for the Wolffian and Müllerian ducts an explanation for the occurrence of dermoid cysts in the ovary. It must be confessed that the structure of many of these cysts suggests that they have an ectodermal origin; but their occurrence in very diverse parts of the body shows that they do not require a normal ingrowth of ectodermal cells into the region in which they arise. Thus in the dermoid cysts which are occasionally found back of the optic bulb, the translocation must be regarded as purely adventitious.[1]

The suggestion has recently been made by Sutton ('86, p. 344), that testicular and ovarian carcinomata are to be explained by the occurrence of degenerating ducts in the neighborhood of the genital ridge, and he is inclined to regard the Wolffian duct as the means of transporting ectodermal cells to this region. The weight of evidence seems to favor the view that carcinomata cannot develop without an epithelial basis (Klebs, '89, p. 771); but this fact does not compel us to seek an ectodermal source for these growths. In the case of adenomata, which also require an epithelial basis, one can see more readily the source of the proliferation; and these abound in the ovary. The germinal epithelium, in consequence of its retention of embryonic characters, seems to be well adapted to the formation of carcinomata, and, according to Birch-Hirschfeld's ('89, p. 202) enumeration, they are somewhat more frequent in the

[1] Many dermoids may be explained as cases of *fœtus in fœtu*, and those in the ovary may often be due to extra-uterine gestation.

ovary than in the testis, even though the latter organ is in such intimate relations with degenerating Wolffian canals.

The remaining portion of the present paper will be concerned with those inferences of a general nature which can be drawn from the development of the pronephros and segmental duct as traced in the preceding pages. These general conclusions naturally fall into two groups: (1) such as are of principal interest in elucidating the development of the excretory system, and (2) such as tend to throw light on the development of the Vertebrate type. Following this division, then, in our discussion, I shall consider in the present section the organogenetic conclusions; and, in concluding, deal with the phylogenetic conclusions which seem to me warrranted by our present knowledge.

In the historical review of the development of the pronephros, it proved in several groups very difficult to draw a sharp line between the pronephros and the mesonephros, and it was suggested at that point in the discussion that this difficulty is in reality a fundamental one, and one which is indicative of the true relations between these parts. The question of the serial homology of the pronephros and mesonephros, as it presents itself to the modern student, is to my mind simply this: Are we to regard these two glands as derivatives of one continuous ancestral organ, which at one time extended over all the somites now occupied by each? The answer to this question naturally must come, if at all, by a comparison of the two organs for the purpose of bringing to light their features of similarity and those of contrast. Manifestly they differ in the time of their appearance; indeed, from this circumstance the two glands were distinguished and named; it remains to consider whether they are constructed on the same or on different types.

In endeavoring to furnish an answer to this question, I shall proceed to an anatomical comparison of the glands, taking into consideration both of the principal portions involved, the glomerular and the tubular parts. The glomerulus of the mesonephros resembles the glomus of the pronephros in the following particulars: both are highly vascular structures composed of ramifying blood-vessels and mesenchyme; they project into spaces which are in communication with the exterior by means of excretory conduits; they originate outside of this space, and gain position within it by pushing before them in their growth its epithelial wall, which then persists as an outer covering to the vascular process; they receive branches directly from the aorta; and, finally, they are developed in regions of the body which at least nearly correspond to each other serially,

as is shown by the relations of the glomus and the glomeruli respectively to the aorta, and by the existence of transitional glomeruli (Birds, Crocodilia, Chelonia). On the other hand, the features in which the glomus differs from the glomerulus may be summarized as follows: the glomus lies in the body cavity, instead of projecting into the lumen of a specialized excretory tubule, and it is a continuous structure, instead of consisting of a number of separate parts.

Turning now to the tubular portions of the two glands, one can recognize a number of common characters. In both can be distinguished a longitudinal conduit and transverse canals, the latter communicating with the body cavity by means of ciliated nephrostomes. The longitudinal canal of the two glands is in reality a continuous structure, the segmental duct. Since the pronephric and the mesonephric tubules are similarly related to this continuous duct, it is evident that they must themselves lie in approximately equivalent regions of the body. The metamerism of both glands primitively corresponds to that of the body somites; this feature is apparent from my account of the Amphibian pronephros, and has been proved for the most anterior mesonephric tubules in Amblystoma (see page 261), as well as for the entire series in Selachii and certain other groups. Finally, the cardinal veins give rise to a meshwork of vascular spaces which bathe in a like manner the tubules of the pronephros and mesonephros. In addition to the different ways in which their tubules are related to glomerular structures, the pronephros and mesonephros are unlike, in that the tubules of the former develop in continuity with the duct, while those of the latter join the duct secondarily. The character of the convolution also is different in the two glands. As is evident from the reconstructions (Plates IV. and VIII.) of the pronephros in Rana and Amblystoma, the complication is here mainly due to the convolution of the longitudinal canal (common trunk); whereas in the case of the mesonephros the longitudinal canal (segmental duct) traverses the gland as an almost straight duct, the transverse tubules alone being highly convoluted.

The pronephros and mesonephros, then, present many striking anatomical features of resemblance, but also differ in several respects. I am however of opinion, that the similarities of structure are sufficiently great to make it probable that pronephros and mesonephros have developed from a common beginning. I do not think, however, that such tabulation of the resemblances and differences gives an adequate insight into the true relationships of the structures. In the search for ancestral characters, it is a matter of indifference whether the organ in ques-

tion actually realizes a given character, or merely shows a tendency to assume it, provided in the latter case it can be satisfactorily shown that the realization of the tendency was prevented by intelligible causes. Thus, in the gastrulation of meroblastic eggs, if it be recognized that the great accumulation of yolk renders emboly impossible, the substitution of epiboly in these cases must be regarded as morphologically insignificant.

The question now naturally arises, Are any of the contrasts between pronephros and mesonephros of such a nature that they can be explained as the result of a single modifying influence? As I have already stated, the most marked point of disagreement between the two glands is the difference in time at which they appear. What influences may that factor exert in modifying their development? At the time when the Amphibian mesonephros appears, the myotomes are widely separated from the peritoneum, and the continuous strip of cœlom immediately ventral to the lower boundaries of the protovertebræ in the region of the pronephros does not exist in the region of the body in which the mesonephros develops. In its place is a mass of cells which extends from the dorsal angle of the body cavity upward towards the overlying myotomes. This mass of cells has been regarded as the first rudiment of the mesonephros. The most natural explanation of the condition is that this mass of cells is morphologically not a secondary proliferation from the peritoneum, but is really the last remnant of the mesoderm which formerly connected the dorsal angle of the permanent body cavity with the overlying protovertebræ. The correctness of this interpretation is shown by comparison with the conditions in Selachians and in Amniotes, where, according to the mutually confirmatory accounts of Sedgwick ('80[a]), Van Wijhe ('88[a], '89), Rückert ('88), and Hoffmann ('89), the mesonephric tubules develop from the communicating canal. The first rudiment of each mesonephric tubule is in reality that portion of the primitive mesodermal plate which lies immediately ventral to the protovertebræ, and, corresponds to that portion of the cœlom into which, as shown in Figure 6, the glomus projects, and from which the pronephric tubules emerge. *Each mesonephric fundament, then, presents on its outer side somatic, on its inner, splanchnic mesoderm.* When the fundaments of the mesonephros have been converted into a series of blind tubules, they grow outward and join the segmental duct. This process appears to me to be precisely equivalent to the *somatopleural* evagination, which at an early period gave rise in the anterior region to the nephrostomal tubules of the pronephros. That portion of the differentiated mesonephric tubule into which the

glomerulus projects is of different origin; it is merely a portion of the cœlom, the walls of which are to be understood to be formed as I have just stated in part by somatic, in part by splanchnic mesoderm.

Returning now to the two features in which the glomus was shown to differ from the glomeruli, — viz. situation within the body cavity, and continuity throughout successive somites, — it will be seen that it is impossible to maintain the former as a ground of distinction, since the glomerulus also lies in a detached portion of the cœlom, and that the latter ground is equally untenable because it simply results from the fact that, before the glomeruli appear, the space into which they would otherwise project as a continuous organ has already been broken up into a series of distinct tubes; the glomerular organ is consequently broken up into a corresponding number of separate vascular processes, each of which becomes converted into a Malpighian capsule.

It seems probable, therefore, (1) that the pronephros and mesonephros were primitively alike, and were portions of a single continuous gland; (2) that in Vertebrates which came to lead an independent existence early in life, an anterior portion of the gland and the whole of the duct are differentiated before the posterior part for the immediate purposes of the larva; and (3) that the difference in structure between the two glands is mainly due to their arising at different times relatively to the differentiation of the body cavity and protovertebræ. Applying this conclusion to the tubular portion of the glands, it becomes at once intelligible why the tubules of the mesonephros must of necessity join the duct secondarily. From this standpoint, the existence of convolutions in the common trunk points to a less differentiated condition of the pronephros, in that, for temporary purposes, the longitudinal canal, including the common trunk, subserves at the same time the functions of an efferent duct and of a secreting tubule.

The foregoing explanation of the nature of the pronephros is based upon the assumption that it is developed as a larval excretory organ. In order to justify this position, it will be necessary to consider whether the pronephros is functional in those Vertebrates which, viewed from this standpoint, would seem to require this organ, and in such alone. For the present purpose, two methods of sexual reproduction may be distinguished: (1) that in which the mother spends her energy in producing a large number of offspring, which are early forced to care for themselves; and (2) that in which the mother produces a small number of eggs, and, either by giving to each a large quantity of reserve food yolk, or by nourishing the young embryo within her own body, secures the existence

of her offspring without calling into play their individual activities. In the former class may be reckoned Cyclostomes, Teleosts, Ganoids, Dipnoi, and Amphibia.[1] Omitting from consideration the little known Dipnoi, a functional pronephros appears in all the members of this group without exception, and is most highly developed in those forms (Petromyzon, Amphibia) which pass through a protracted larval stage. The other class includes Selachians, Reptiles, Birds, and Mammals. In every member of this group the pronephros is rudimentary.

I conclude, therefore, that pronephros and mesonephros are parts of one ancestral organ; that the glomeruli are strictly homodynamous with the glomus; that the entire tubular portion of the pronephros is represented in the mesonephros; that the cavity of a Malpighian capsule and the nephrostomal canal connecting it with the body cavity are detached portions of the cœlom, the equivalents of which are not thus differentiated in the pronephros; that the pronephros is developed as a larval excretory organ; and that the period at which it appears largely accounts for its peculiarities of structure. This general conclusion, which is mainly based upon a study of the conditions in Amphibia, is, in my opinion, in perfect harmony with the recorded observations on other groups.

It must be remembered in this connection, however, that the pronephros may possibly have been developed from the primitive excretory organ independently in two or more groups, in response to similar physiological necessities. While I have not been able to preclude this possibility, I am nevertheless inclined to the opinion that in general a closer relation exists, and that consequently the pronephros is homologous throughout all Vertebrates. An interesting condition manifests itself in those forms (Teleosts and Ganoids) in which the pronephros remains functional until the individual is nearly adult. In these the pronephric chamber becomes partially (Lepidosteus) or entirely (Teleosts) cut off from the body cavity and comes to resemble an enormous Malpighian capsule. The region in Crocodilus intermediate between pronephros and mesonephros shows a

[1] In the one group, the eggs are holoblastic, or if meroblastic contain little yolk (Teleosts); in the other, they contain much yolk, or the young are nourished by means of a placenta (Mammals). Mr. Samuel Garman has kindly called my attention to a number of cases in Amphibia where the period of larval life is greatly reduced. The occurrence of holoblastic segmentation in this group appears to me to afford adequate evidence that such conditions are secondary. Moreover, there actually appears to be a reduction of the pronephros in such species as abandon in part their larval life. In the case of Hylodes martinicensis, mentioned by Mr. Garman in this connection, Selenka ('82) has shown the pronephros to be very degenerate.

similar differentiation of a part of the cœlom into a distinct excretory chamber. The condition in this region differs from that of the mesonephros of this genus solely in the circumstance that the excretory chamber is not broken up into metameric portions; this process takes place in the posterior region, and produces a typical mesonephros.

It now remains for me to review the opinions of previous writers in respect to the nature of the pronephros. The existence of a larval excretory system different from and earlier than the mesonephros appears to have been first suggested by Marcussen ('51); but this view received no recognition until it had been reasserted by Wilh. Müller ('75), who gave to the pronephros a distinctive name, *Vorniere*. Semper ('75), on the other hand, denied utterly the nephridial nature of the pronephros, and regarded the glomus as equivalent to the suprarenals (Nebennieren) of Plagiostomes. Fürbringer ('78[a]) vigorously opposed this view, and maintained that the pronephros and its duct represent a primitive excretory system which conspicuously differs from both mesonephros and metanephros. According to Balfour's ('75) earlier view the segmental duct is formed by the backward growth of a single anterior evagination, which may be regarded as the representative of a mesonephric tubule. He ('81) later interpreted the pronephros similarly to Fürbringer, but was still inclined to believe that each mesonephric tubule was "in a sort of way serially homologous with the primitive pronephros." It is very difficult for me to reconcile the latter opinion with his view that the pronephros is a primitive excretory system derived from Plathelminthes, while the mesonephros is a secondary (new) development which does not appear until the trunk becomes segmented. Moreover, this view manifestly ignores the metamerism which is exhibited by the pronephros. It appears to me therefore entirely unsatisfactory.

Sedgwick ('81) first distinctly stated the conclusion that the pronephros and mesonephros are differentiations of a single ancestral organ. This view, which was adopted by Renson ('83), does not seem to have been generally accepted, although several authors, by describing what they denominate a transitional region, seem to me implicitly to assume an intimate connection between the two glands. Mihalkovics ('85, pp. 65, 66) denied that they are *wholly* homologous, on the ground that the pronephric tubules are peritoneal evaginations, whereas those of the mesonephros are differentiated in the solid Wolffian blastema. Mihalkovics does not explain *his* use of the term *complete* homology, and I have been unable to satisfy myself in regard to the precise relations which he supposed to exist between the two glands.

Van Wijhe ('88[a], '89), Rückert ('88), Hoffmann ('89), and Wiedersheim ('90), have distinctly denied the serial homology of the pronephros and the mesonephros. The objections of these authors to the view which I have adopted have been most clearly formulated by van Wijhe ('89, pp. 509, 510), whose account I shall follow in my criticism of their position. First, "the pronephros arises before the appearance of the duct or the mesonephros, and is indeed the first part of the excretory system that appears." This point of difference is, as I have stated, the most conspicuous feature in which the two glands are unlike. It is, however, not a weighty argument against their serial homology. Secondly, "the pronephros arises as an (in Selachii segmented) evagination of the somatopleure; its cavity, which may be temporarily obliterated by the proliferation of the walls, is formed as an evagination of the body cavity (Metacölom). The mesonephros, on the other hand, is not formed as an evagination, and it is constituted of somatopleure as well as of splanchnopleure." This analysis seems at first sight to establish a fundamental contrast between the pronephros and the mesonephros, and I admit fully the cogency of the argument in disproving a comparison of the nephrostomal and glomerular portions of a mesonephric tubule with the nephrostomal canal of the pronephros. On the other hand, however, I would insist that a hitherto unnoticed homologue of the pronephric evaginations is to be found in the *outward growth* of the primitive mesonephric canal to join the duct.[1] (See page 301.) It is in precisely this way that a tendency to a somatopleural evagination would of necessity manifest itself. Thirdly, "the duct always appears in continuity with the pronephros, but always discontinuous with the mesonephros, which only secondarily fuses with it and empties into it." This circumstance, as I have already shown, is a direct consequence of the condition explained under the first head. Fourthly, "the mesonephros possesses Malpighian corpuscles; while the pronephros has none, the glomus of the latter not being homodynamous with the glomeruli of the mesonephros because it is a vascular tuft invaginated into the secondary body cavity (Metacölom)." This contrast appears to me morphologically inaccurate, as I believe I have adequately shown in the preceding discussion.

A further objection, which van Wijhe does not mention in his enumeration, is the occurrence of rudimentary mesonephric tubules in the somites which formerly gave rise to the pronephros. To prove this assertion, it

[1] This is the only portion of the mesonephric tubule which can properly be called an evagination; the entire tubule comprises the evagination plus the communicating canal.

is usually regarded adequate to show the existence in the pronephric region of metameric diverticula proceeding from the body cavity towards the overlying protovertebræ. These diverticula are the communicating canals, and it is undoubtedly true that from similar canals in the posterior region mesonephric tubules are actually developed; but, to my mind, the occurrence of these diverticula in the pronephric region cannot be brought forward as evidence of the existence of two sets of nephridial tubules in these somites, until it can be shown that these remnants of the canal-like communication between protovertebræ and lateral plates exhibit some indication of the characteristic nephridial differentiation. i. e. grow outward and join the duct. This, I believe, has never been *demonstrated*. The existence of such a growth has, however, been asserted by several observers; but it seems to me compatible with the view I have expressed of the relations between pronephros and mesonephros. Since the time of the investigations of Balfour and of Semper on Selachians, it has been a familiar fact, that, although at first only one mesonephric tubule occurs in each somite, the further complication of the gland is largely produced by the formation of new tubules which proceed from the region of the primary Malpighian capsule. If the development of more than one tubule in a somite became normal in the ancestors of the Craniotes before the separation of pronephros and mesonephros took place, the development of such secondary tubules in the pronephric region would at once be intelligible.

A more fundamental objection is contained in an ignored observation of Gasser ('82, p. 96) on Alytes, according to which a typical glomus is developed in the body cavity of the mesonephric region, in addition to the universally present glomeruli. Gasser's account is contained in a rather short note unaccompanied by figures; it has not been confirmed by any subsequent observer; nor have I been able to find such a structure in either Rana or Amblystoma. I am therefore inclined to the opinion that Gasser may have mistaken for the glomus either the germinal ridge or the fat-body, both of which are developed in this region, although this explanation would contradict the statement of Gasser that the mesonephric glomus is a transitory organ. Be that as it may, I cannot without further evidence accept his account as final.

Semon ('90) has recently asserted that the pronephros and mesonephros are built upon the same structural type. He was led to this conclusion by a study of the excretory system in Ichthyophis. I have already alluded to the condition of the pronephros in this form. It is characterized by the possession of a completely closed pronephric cham-

ber, from which a portion of the nephrostomes ("inner" nephrostomes) emerge. Each nephrostomal canal, however near the nephrostomal end, is joined by a branch which communicates with the permanent body cavity by means of an "outer" nephrostome. According to Semon, the pronephric chamber, as well as the cavity of a mesonephric Malpighian capsule, is a diverticulum of the cœlom; and the nephrostomal canal which joins the glomerular portion of a mesonephric tubule with the body cavity is represented by those canals of the pronephros which emerge from the open body cavity. The mesonephros is to be regarded as a "generation" of excretory tubules younger than the pronephros, and the latter may be conceived to have primitively extended throughout the entire trunk. In many features Semon's view is similar to that expressed in the preceding pages. The point of difference which I would here emphasize is the different way in which the nephrostomal canal of the mesonephros is explained. According to my opinion, *this canal is a remnant of the communication between the protovertebral cavity and the secondary body cavity, and is not represented in the tubular portion of the pronephros.* Semon, on the other hand, claims that it is the homologue of the outer series of nephrostomal canals in the pronephros of Ichthyophis. Considering the relations of the glands in that form alone, this view seems well justified; but it neglects the significant relation which has recently been shown to exist between the mesonephros and the communicating canal; and I am of opinion that the view as applied to other Vertebrates is untenable, unless it can be shown that the outer nephrostomal tubule of the Gymnophionian pronephros also develops from that canal. The latter interpretation is, I must admit, at least possible; but we must await further researches on the development of these Amphibia before accepting such a conclusion.

The closing section of this discussion will be devoted to a consideration of the evidence which the development of the excretory system as a whole throws on the origin of Vertebrates.

Two methods of investigation, which are mutually dependent, yet quite unlike in their application, may be employed in attempting to draw phylogenetic conclusions. One of these methods is peculiar to embryological research; it is dependent upon the principle that ontogeny is in part an abbreviated recapitulation of phylogeny; its method is to eliminate cœnogenetic characters; it accomplishes this largely by the aid of a physiological estimate of the influences of larval and embryonic environment, and it is comparative only throughout

the extent of the group whose origin is sought. The other method is common both to comparative embryology and to comparative anatomy; it is dependent upon the inherent improbability of the same physiological requirements, being met by the same structural device in two groups which are not genetically related; it can employ equally well, though with a somewhat different significance, both cœnogenetic and palingenetic characters; it is purely anatomical in its method, and it is in the broadest sense comparative. The first I may designate as the method of elimination, or the intensive method; the latter as the comparative, or extensive method.

I have been led to make the preceding analysis in order to employ the division thus indicated in the subsequent discussion, and also because it is a contrast which does not appear to be generally recognized. Thus, a recent text-book of zoölogy (Hatschek, '88, pp. 25, 26) identifies the methods of embryology with those of comparative anatomy, and declares that palingenetic and cœnogenetic characters are equally valuable for phylogenetic inferences. According to the preceding analysis, these two statements are partial, relating only to the comparative method in embryology, and ignore the higher use which renders embryological facts of peculiar value.

Observing then this two-fold division in the following discussion, an attempt will first be made to reconstruct from the ontogeny of Vertebrates the ancestral history of their excretory organs.

The most general character which appears to be common to the ontogeny of all Vertebrates is the intimate relation which exists between the excretory tubules and the cœlom. This relation is peculiarly well illustrated by the pronephros, but it is true also of all the urogenital organs, and is a fact which in my opinion throws considerable light on their evolution. The cœlom appears to be an internal cavity developed to meet a number of physiological needs. It is likely that in the lower Invertebrates the cœlom served largely a nutritive function (see, e. g., Chun, '80, pp. 248–253); but I am of opinion that in the higher Invertebrates and in Vertebrates the cœlom early became in large measure an excretory space. This function of the cœlom, inferred from its relations with nephridia, is in accord with its situation in the body. Evidently the organs which would be most in need of a near place of discharge for nitrogenous waste products are those which are in the highest degree metabolic. Such are, *par excellence*, the muscle masses of the body, and it is a familiar circumstance that in all Chordates the primitive muscle plates develop from the lining wall of the dorsal segmented por-

tion of the cœlom. It is very probable that this arrangement represents the earliest differentiation of a special excretory surface of which evidence is preserved in the ontogeny of Vertebrates.

The next step in the specialization of the urinary organs is the establishment of definite conduits for the purpose of conveying the excreted products to the outside. It is possible that simple apertures, such as the abdominal pores, at first served this end; or, if the enterocœlous condition represent a phylogenetic stage, communications with the intestinal tube may have afforded an outlet to the excreted fluids. Be this as it may, it is evident that the ancestors of our present Vertebrates early acquired specialized tubes subserving this purpose.

In the account of the development of the Amphibian pronephros and duct given in the first section of the present paper, emphasis was laid upon the fact that these structures are differentiated from a solid somatopleural thickening, and do not arise as a fold of the peritoneum. Manifestly the former condition is cœnogenetic; such a solid thickening could in no wise function as an excretory conduit. On the other hand, it must not be rashly assumed that the somatopleural thickening is a disguised *fold* of that layer. On the contrary, the pronephros, on canalization, shows itself to be already composed of a series of metameric evaginations of the cœlom, and it is perfectly conceivable that the pronephric thickening is a modification from a condition where the separate evaginations had their *independent* means of communication with the exterior, the several diverticula being fused into a solid mass. Either interpretation would be physiologically intelligible. In the first case, a certain region of the peritoneum would first sink as a groove into the parietes of the cœlom. This channel might, like the nephrostomes, be provided with vibratile cilia, and might thus serve to carry the fluids lodged in it back to a single pair of orifices situated near the posterior end of the cœlom. As a further differentiation, it is to be conceived that this groove became at intervals constricted off from the cœlom, forming a retroperitoneal duct with a series of nephrostomal tubules.

According to the second alternative, it is necessary to suppose that the several evaginations communicated distally either directly with the exterior or with an independent longitudinal duct. The nephridia of Heteromastus and Capitella (Eisig, '88, pp. 242, 272), in which no external opening is present, show us that the gradational steps in the formation of such outgrowths may be conceived to be functional.

In judging between the two views to which allusion has just been made, it is important to consider whether the ontogeny of other groups

ever presents either of these processes in an unambiguous manner. I have already expressed my doubts in regard to the development of the pronephros and duct by the incomplete closure of a groove of somatopleure. The best attested claim that has been made for such a mode of origin was that made by Goette, Fürbringer, Hoffmann, and Marshall and Bles, for Amphibia; but this position is distinctly contradicted by my own observations. Indeed, this mode of origin has been recently denied in the case of every class except Teleosts, a group in which it is very difficult to obtain accurate evidence respecting the early history of the mesoderm.

On the other hand, numerous recent investigators have described the first rudiment of the pronephros as a series of distinct evaginations. Such observations have been recorded in Cyclostomes by Kupffer ('88), in Ganoids by Beard ('89), and in Amniotes by almost all writers on their early development. It seems to me, therefore, that the mode of formation by means of serial evaginations has a far wider distribution, and is more clearly attested, than that by means of an incompletely closed fold. I am of opinion that the condition in Amphibia and Selachia is to be regarded as derived from such evaginations by means of cœnogenetic modification; and that the weight of internal evidence is in favor of the view that the tubules were primitively distinct.

Typically the nephridial tubes are strictly metameric, one pair of tubules being developed in each metamere. The occurrence of several nephridia in a somite occurs, as we have seen, in the case of the mesonephros of certain Amphibia. This condition seems to me to be a character secondarily acquired. The following reasons confirm this opinion: (1.) In other forms, the strict metamerism of the nephridia is the earliest ontogenetic condition, the duplication of the tubules appearing much later. (2.) The dysmetameric arrangement seems to be correlated with the limited number of somites which are, in such cases, involved in the formation of the mesonephros; thus, in the Anura, a group in which the number of trunk somites is extremely small, the mesonephros departs most widely from the metameric condition; in Urodeles, the number of somites is larger, and there is an indication of metamerism in the anterior tubules; and again in Cœcilia, where the number of somites is still larger, the mesonephros has the typical metameric arrangement. (3.) The pronephros, which in general represents the least modified portion of the excretory system, retains a metameric condition in those forms in which this arrangement is absent in the mesonephros.

In order to ascertain the probable mode in which the metameric diver-

ticula primitively terminated, whether they opened on the surface or joined a longitudinal duct, it will be necessary to consider the pronephros alone, since the segmental duct is already present before the mesonephros is formed, and we cannot expect to find an adequate criterion for determining whether the union of the mesonephric tubes with the duct be primitive or secondary. In the pronephros there is in most cases no evidence of a mode of termination more primitive than that of communicating with a duct. Two arguments, however, occur to me, which seem to indicate that a series of direct outlets to the exterior may have been early present. In the first place, the pronephric diverticula have frequently been observed to enter into intimate union with the ectoderm. Thus Rückert ('88, p. 217) was led to believe that the pronephric thickening of Selachians even received a contribution of cells from the outer germ layer. The most natural explanation of this condition seems to me to be, that the fusion of the diverticula with the ectoderm is the recapitulation in the ontogeny of a phylogenetic stage, which possessed nephridia provided with direct openings to the exterior. Secondly, Amphioxus, according to the most recent investigations, is provided with a series of nephridia opening into the atrial chamber, which latter we are, in my opinion, justified in regarding as a simple infolded portion of the exterior. Accepting the homology of the nephridia of Amphioxus and those of Craniotes, it seems to me probable that the ancestors of Vertebrates possessed nephridia which resembled those of Amphioxus in opening directly to the exterior.

If separate diverticula leading from the cœlom to the exterior be the primitive condition of the Vertebrate excretory organs, we have still to seek the origin of the segmental duct. On this point, the pronephros alone can afford evidence. The participation of the ectoderm maintained by many authors for the posterior end of the duct affords the suggestion that it may have first been formed as a groove of that layer, or that a primitive anterior opening was gradually shifted back to the cloaca. It may be objected to this view, (1) that in many Vertebrates no participation of the ectoderm occurs, while in none has it been shown that the mesoderm does not play a part in the formation of both anterior and posterior portions of the duct; and (2) that the longitudinal canal of the pronephros, which forms the anterior prolongation of the duct, in no case arises in this way. In the pronephros the longitudinal canal arises, as testified by a large number of recent investigators for divers groups, and as confirmed by my own observations on Amphibia, by the fusion of the distal ends of the pronephric diverticula. This mode of development

seems to me entirely in harmony with physiological requirements; and in this earliest fragment of the excretory system we have, in my opinion, a remnant of the primitive mode of formation of the segmental duct.

The question at once arises whether there is any indication of this mode of origin preserved in the development of the posterior portion of the duct. A free backward growth, such as is maintained for many Vertebrates, is evidently far removed from the primitive mode of formation, and is to be regarded as an adaptation to the needs of the pronephros. The origin of the duct *in situ* from a somatopleural proliferation is without doubt a modified condition; yet it suggests a mode of origin which is in agreement with that observed in the anterior region. I have already emphasized the circumstance that in Amphibia the duct arises from a mass of cells which is perfectly continuous with that from which the pronephric tubules are differentiated; and it is possible that both regions represent disguised nephridial evaginations of which those in the posterior region are never differentiated as actual canals except in such portions as are converted into the duct. Further evidence in favor of this view is afforded by the occasional occurrence of supernumerary pronephric tubules such as have been observed by Mollier ('90, p. 224) and myself (page 253). The acceptance of this interpretation would necessitate a modification of our conception of the relations between pronephros and mesonephros, since we should be obliged to regard the mesonephric tubules as a second generation of tubules, the first generation having been employed in giving rise to the duct. On the other hand, it is quite possible that the entire backward growth of the duct is a *wholly* secondary process to meet the needs of a prematurely developed portion of the primitive excretory organ. This is the only interpretation which seems admissible in those cases where the duct has been found to grow backward free from adjacent tissue.

The conception of the phylogeny of the duct which I have just presented offers a partial explanation of the contradictory evidence which has been advanced respecting the germ layer from which the duct arises. With a narrower conception of the phylogeny of the duct, it is difficult to understand why the ectoderm should participate in the formation of the excretory system in one group, but not in another, and why the posterior end of the duct should in some cases be formed at the expense of a germinal layer different from that which gives rise to its anterior portion and to the nephrostomal canals wherever they appear. If, however, we assume the existence of a phylogenetic stage in which a series of nephridia open directly to the exterior, it is at once evident that a

very trifling difference of location would determine whether the longitudinal canal, by means of which the duct arises, should develop from the mesoderm or from the ectoderm. It is to be remarked, however, that such an explanation is not wholly satisfactory, since one would expect on this hypothesis that those forms in which the ectodermal origin of the duct seems well attested would show evidence of close genetic relationship, while those classes in which the duct arises from the mesoderm ought to form an equally well defined group. This condition, however, is by no means realized. On the other hand, the force of this objection is materially weakened if we regard the duct as a recent acquisition, which its absence in Amphioxus gives some justification for assuming. The explanation seems to me, nevertheless, in a measure unsatisfactory, and I have adduced it merely as a possible solution of the problem to which the apparently diverse relations of the duct to the germ layers gives rise.

An intimate relation is always very early established between the excretory tubules and the cardinal veins. Such an arrangement is so favorable for the process of secretion that there can be but little doubt that this condition prevailed in the ancestors of all Vertebrates. There does not appear to be any evidence which would indicate whether the cardinal veins or the excretory tubules are the more primitive structures.

In addition to the means of excretion afforded by the epithelial walls of the tubules, the Vertebrate kidney-organs possess peculiar glomerular structures. These, as I have already shown, are all formed on the type of the pronephric glomus. In their primitive condition, they consist of vascular tufts, which receive blood from the aorta and project into the body cavity from the root of the mesentery.[1] The origin of such a primitive glomerular structure is not far to seek. It is readily conceivable that fluid may at first have simply exuded from the aorta, and, traversing the small amount of tissue intervening between it and the body cavity, may have reached the orifices of the excretory tubes prior to the development of any specialized organ subserving a glomerular function. This process being once established, any modification of structure which should allow a portion of the aortic current to be brought into closer relations with the excretory tubules would be of obvious utility, and would be preserved.

The excretory system thus constituted would represent the proneph-

[1] The view of the excretory system here presented explains the double blood supply of the kidneys of lower Vertebrates, and also the circumstance that the Malpighian bodies always receive their blood by a direct branch from the aorta.

ric type of structure. I have already sketched the manner in which the mesonephros may be derived from the pronephros by supposing the metameric segmentation of the body to extend to that portion of the cœlom from which the nephrostomes emerge. The account given in the preceding section of this paper regarded the tubules as passive in such a metamorphosis. It is possible, however, that the transference of the tubules to a segmented portion of the cœlom may have been in part effected by a dorsalward shifting of the nephrostomes. In either case, I am of opinion that the mode of development which I have now suggested is applicable alike to the pronephros and the mesonephros, and I may also add to the metanephros (see Sedgwick, '80).

I have now presented, in a suggestive manner rather than as a complete argument, certain indications of the phylogeny of the excretory system which may be obtained from internal evidence. It still remains for us to consider what conclusions are justified by a comparative study of the excretory system, and whether the phylogenetic stages suggested in the foregoing account are to be found in any group of living animals.

The sole purpose of this discussion is to ascertain the most probable phylogenetic line of development for the excretory system of Vertebrates. For this reason, I shall avoid any discussion, which would necessarily be lengthy, respecting the interrelationships of the diverse excretory organs found in Invertebrates, simply endeavoring to seek out those classes which possess nephridia similar to those of Vertebrates, and shall ignore the further consequences which would follow from the assumption of a homology in any single case.

In the preceding account, I have provisionally accepted the view that Amphioxus belongs to the Vertebrate phylum, and have endeavored to interpret its kidneys in accordance with that view. With Tunicates it is quite different; not merely do they afford no assistance in the solution of the problem in hand, but it has hitherto proved impossible to find any organs in this group which can be regarded as homologous to Vertebrate nephridia.[1] In my opinion, it cannot be objected that the absence of such organs in Tunicates proves that the Vertebrate nephridia arose within the Vertebrate phylum. A rigid adherence to such a system of restriction in the case of other organs would quickly lead to absurd conclusions.

The only classes of animals in which we need seek for a homology of

[1] Hatschek ('84, p. 519) regarded the single nephridium described by him in Amphioxus homologous with the neural gland of Tunicates; but I have already pointed out the probable inaccuracy of this observation.

the Vertebrate renal organs are those belonging to the bilateral cladus; and among these I shall consider only those forms which are usually included in the rather heterogeneous class Vermes. This restriction is justified by the circumstance that the only similarities of structure which are to be found between the excretory system of Vertebrates and those of Mollusks and Arthropods recur with greater force in the case of several groups of Vermes.

In comparing the kidneys of Vertebrates and those of Worms, I shall distinguish three types of structure in the latter group: (1) the water-vascular system of Plathelminthes, (2) the excretory system of Nemertines, and (3) the nephridia of Annelids. The various organs which serve as excretory and genital passages in Rotifers, Nematodes, Echiurids, and Sipunculids are either referable to one of these types, or are valueless for the purpose in hand.

In endeavoring to find what points of similarity exist between the excretory system of Plathelminthes and that of Vertebrates, I have been unable to formulate any more definite statement than that both consist of longitudinal internal canals, which bear numerous lateral branches, and which open directly or indirectly to the exterior. On the contrary, the two sets of organs appear to me to perform the function of excretion by anatomical devices which are diametrically opposed. In Vertebrates, the excretions are either (primitively) poured into the cœlom and conveyed thence by a simple series of conduits, or excreted from the blood in the course of the tubuli uriniferi of the kidneys. In Plathelminthes, on the other hand, the excretory tubes ramify throughout the entire body parenchyme, and, so to speak, seek out the waste products of metabolism at the seat of their formation. It is a contrast such as exists between lungs and tracheæ, and appears to me of fundamental importance. According to Fraipont ('80) and Francotte ('81 and '83, pp. 734, 735), it is true, there is a communication between the excretory tubules of Plathelminthes and certain interior canalicular spaces, which they interpret as a rudimentary cœlom. The evidence in favor of the latter interpretation is certainly far from complete, but could not, if true, overthrow the fundamental contrast which I have just emphasized. Furthermore, I am not aware that any subsequent writers have confirmed this account of the termination of the excretory capillaries; while Pintner ('80, p. 302), von Graff ('82[a], pp. 106 *et seq.*, '82[b], p. 80), Lang ('81, p. 208, '84, p. 167), Iijima ('84, p. 400), Zschokke ('87, p. 165), and Böhmig ('90, p. 243) have all asserted that the terminal sacs are entirely closed. The conclusion seems warranted that no direct evi-

dence in support of an intimate relation between Vertebrates and Plathelminthes is afforded by a comparison of their excretory organs.

In Nemertines the excretory system is in peculiar relations with the blood vascular system. According to Oudemans ('85), the excretory system of the Schizonemertini and the Hoplomertini consists of a longitudinal tube, which is closely applied to the lateral longitudinal blood-vessel of the œsophageal region, and this tube communicates with the exterior by means of a single excretory pore or by a number of such openings. In Carinella and Carinoma, however, the connection is much more intimate, and the glandular portion of the excretory organ lies embedded in the œsophageal blood lacunæ and communicates with the latter by means of two or three evident openings. Oudemans asserts, indeed, that the excretory system is in reality a detached portion of the blood vascular system. Bürger ('90, p. 92), however, has recently thrown some doubt upon the existence of open communications between the nephridia and the blood-vessels, but reaffirms the close dependence of the excretory system upon the vascular trunks.

Comparing the nephridia of Nemertines with those of Vertebrates, it seems to me that one cannot fail to recognize a pronounced difference in type. In Vertebrates the nephridia are canals in close relation with the cœlom; they develop from its epithelium, and even in the adult arise from chambers which must be regarded as detached portions of the cœlom. The excretory organs of Nemertines lie between the vascular trunks and the exterior, and show no such relations with the cœlom.

Among the Annelids, on the other hand, the Chætopods possess an excretory system, which seems to present several features of strong resemblance with the nephridia of Vertebrates, and it remains to be considered whether an actual homology can be postulated in this case.

The points of similarity may for the present purpose be classed under seven heads. (1.) The Vertebrate and the Chætopod excretory systems agree in the fact that both primitively serve, at least in part, to convey to the exterior such fluids as accumulate in the cœlom, this cavity being used as a capacious excretory reservoir. (2.) In both groups certain portions of the epithelial lining of the cœlom become differentiated into specialized excretory glands. In Vertebrates the only structures of this character are the glomi and glomeruli; but in Annelids there is evidence that considerable areas of the peritoneum may become modified in this way. It was suggested by Claparède ('69, p. 615), that the chloragogen cells secrete certain elements from the blood and transfer them to the perivisceral fluid. This view of the function of the chloragogen cells has

been confirmed by a large number of observers,[1] and it has been further shown that individual cells, having become charged with excreted concrements, loosen from the layer to which they belong, and float freely in the cœlom, whence they are discharged through the nephridia. The chloragogen layer covering the blood-vessels appears moreover from its anatomical relations to be a portion of the visceral mesoderm, and it has been shown to arise ontogenetically from that layer (Roule, '89, pp. 201, 252, 290). The chloragogen cells are frequently distributed upon special vascular processes, thus forming distinct glandular organs. Similar in function is probably the glandular envelope of the ventral vessel in Polyophthalamus (E. Meyer, '82, p. 816), and cases may be found among Polychætes in which definite peritoneal glands are present (Grobben, '88, pp. 255 *et seq.*, Eisig, '87, pp. 227, 245, 681). I should not wish to assert a strict homology between the glomus and the masses of chloragogen cells ; yet it seems to me likely that the latter represent an early differentiation of the splanchnic mesoderm of which we have more specialized developments both in Annelids and in Vertebrates.[2] (3.) The efferent conduits take their origin from the cœlom by means of a series of ciliated funnel-shaped openings, the nephrostomes. (4.) The nephrostomes lead into transverse convoluted canals, along the course of which a large part of the excretion takes place. (5.) The nephridial tubes arise from the parietal peritoneum. (6.) They are typically strictly metameric, one pair of tubules being developed in each metamere. The deviation from this typical metamerism to which I have already referred in the case of Vertebrates is paralleled by similar conditions in Capitella (Eisig, '87, p. 594). (7.) The development of the Chætopod nephridia resembles in general that shown by those of Vertebrates. Both the pronephric and mesonephric tubules arise as a series of metameric outgrowths from the somatic mesoderm. In Polychætes this is evidently the mode of origin of the nephridia. In Oligochætes the development is more doubtful, but the method of origin described by Bergh ('90) is in essence the same as that known in Polychætes, and the mode of development maintained by Wilson ('87, pp. 185, 186, and '89, pp. 419 *et seq.*) may be interpreted so as not to be in fundamental opposition with such a method.

There is one feature in regard to which the nephridia of most Anne-

[1] E. g. Timm ('83, pp. 122, 123); Kükenthal ('85, p. 336); Meyer ('87, p. 648).

[2] A further analogy is possibly to be found in the fact that in Amphibia certain cells early loosen from the wall of glomus and fall into the cœlom, leaving intervals between the remaining cells of the epithelium.

lids and those of Vertebrates differ conspicuously, viz. in the mode in which the nephridia terminate. It is a familiar fact, that in Annelids each nephridium opens separately on the surface of the body; while in Vertebrates the nephrostomal tubules all connect with a pair of longitudinal ducts opening into the cloaca. In commenting upon this feature of difference, it is important to note in the first place that the contrast is not of universal application. It has been recently shown by E. Meyer ('87, pp. 618–625) and Cunningham ('87[a], 87[b], pp. 248–253) that in Lanice conchilega, a terebelloid Annelid, certain nephridia open into a longitudinal trunk, and only secondarily communicate with the exterior. On the other hand, it is probable that Amphioxus possesses nephridia which open to the exterior (atria cavity) without the intervention of a longitudinal duct. If such differences can occur among the members of either group, it seems to me that it would be unjust to deny the homology of the other portions of the system in consequence of the fact that Vertebrates *in general* possess a longitudinal duct, while Annelids *in general* do not. It appears to me, moreover, that the condition of the nephridia in Lanice conchilega and the ontogeny of Vertebrates both serve to indicate the manner in which the duct may have secondarily arisen. In Lanice conchilega there is no doubt that the nephridial duct is a secondary growth, and it is highly probable that the channel is formed by outgrowths extending from each of the nephridial tubes backward and communicating with the next following nephridium. Two groups of nephridia can be distinguished in Lanice conchilega. The more anterior of these consists of a short longitudinal duct which bears three nephrostomal tubules, and terminates at its posterior end by a single pore. In the posterior set, the longitudinal duct is merely a canal which connects the several nephridia, while these continue to retain their external orifices. I have already pointed out that the ontogeny of Vertebrates presents a similar process in the development of the longitudinal canal of the pronephros, and have shown that such changes may likewise have taken place in the region of the mesonephros. I by no means wish to imply by this comparison a belief that the ordinary mode of development in Vertebrates is to be directly derived from that presented by Lanice conchilega, nor to assume a close genetic relation between Vertebrates and genera presenting this condition. I merely wished to emphasize the fact, that in Lanice conchilega we have an instance of a species which, primitively possessing discrete nephridia, such as may have been present in the ancestor of Vertebrates, has acquired a longitudinal excretory canal by a process of transforma-

tion which resembles that by which Vertebrates acquire in their ontogeny the segmental duct.

From the facts thus far brought forward, I conclude, (1) that the group of animals which presents nephridia most closely resembling those of Vertebrates is unquestionably that of the Chætopod Annelids; and (2) that the Vertebrate excretory system can be readily derived from that of Annelids by a series of steps which are in accord with the evidence afforded by the ontogeny of Vertebrates.

In conclusion, I shall briefly allude to the opinions of previous writers respecting the origin of the Vertebrate excretory organs. These opinions fall, in the first place, into two classes, according to one of which the excretory system is derived from Invertebrate ancestors; according to the other, it has arisen wholly within the Vertebrate phylum.

The most recent exponent of the latter view is van Wijhe ('89, pp. 506 *et seq.*). The arguments offered by this author in support of his position are in part dependent upon his denial of the serial homology of pronephros and mesonephros. Van Wijhe also employs two arguments which are independent of his position in regard to this point: (1) nephridia are absent in Amphioxus, and therefore the common ancestral form cannot have possessed them; (2) the renal organs do not appear until after the so-called "Acrania stage," and therefore could not have appeared phylogenetically until this stage had been passed. Granting both premises, it seems to me that neither conclusion follows. With reference to the absence of kidneys in Amphioxus, the possibility — or should I not say probability? — of extensive degenerative modification is entirely neglected. Moreover, it has now been rendered probable that true nephridia do exist in Amphioxus, an observation which removes at a blow the whole basis of the argument. I do not believe many embryologists would unite with van Wijhe in holding that characters which appear simultaneously in the ontogeny of a form must necessarily have arisen contemporaneously in its ontogeny. For my part, I am unable to diagnose with accuracy the "Acrania stage" of Amphibia; but Ostroumoff ('88, pp. 77, 78) appears to have had the necessary insight, and denies emphatically that the pronephros in the case of Reptiles arises after the "Acrania stage."

Turning now to the hypotheses that have been advanced involving the derivation of the Vertebrate excretory system from Invertebrate ancestors, Haeckel ('74, p. 37), Gegenbaur ('78, p. 628), and Fürbringer ('78[a], pp. 95 *et seq.*) endeavored to show that the Vertebrate nephridia were derived from those of Plathelminthes. Semper and Balfour, on the

other hand, claimed that the transverse tubules of the mesonephros are homologous with the segmental tubes of Annelids, an opinion which is shared by Beard, Haddon, Kollmann ('82[a]) and others.

Rückert ('88, p. 262) has recently denied this homology, and asserted that the Annelidan nephridia are represented in the pronephros alone, since the latter is the only portion of the system of metameric tubes which comes in contact with the ectoderm. With Rückert, I would admit that the evidences of an Annelidan origin of the excretory system are to be sought mainly in the pronephros; but, in view of the intimate relations which exist between pronephros and mesonephros, it seems to me more probable that both have had the same phylogenetic origin. Ostroumoff ('88, pp. 80 *et seq.*) also has asserted that the development of the pronephros indicated that this system had been inherited from Annelidan ancestors.

On the other hand, a number of authors maintain that, although the mesonephros may be derived from the segmental organs of Annelids, the pronephric system is represented by other Invertebrate nephridia. Thus, Semper ('76, pp. 387, 388) suggests the possibility that the duct (pronephric system so far as present in Selachians [1]) may represent the unsegmented excretory tubules developed in the larva of Nephelis, or may even represent an inheritance from the Plathelminthan water-vascular system; and Balfour ('81, p. 607) was led to accept this view.

In addition to his hypothesis of an origin of the excretory system of Vertebrates from that of Plathelminthes, Fürbringer suggests the possibility that the entire system may have arisen from Gephyreans, in which unsegmented and segmented excretory organs are stated to coexist. This view was adopted by Kollmann ('82[a]), and is offered as a suggestion in Wiedersheim's ('86, p. 731) text-book.

None of the views which claim a *double* origin for the excretory system seem to me to be tenable, in consequence of the fact that the pronephros, an undoubtedly segmented element, develops in *strict continuity* with the duct, the so-called unsegmented element. The view according to which the excretory system is derived from that of Gephyreans, moreover, is liable to special criticism. This claim that Gephyreans present an excretory system of a double nature, segmented and unsegmented, doubtless refers to the coexistence of two or three pairs of nephridia, together with the so-called Analschläuche of Echiurids. I am unable to see the slightest evidence that the Vertebrate excretory system is made

[1] By this suggestion, Semper allows some justification to W. Müller's conception of a pronephros, although he had earlier contested it.

up of such remote parts; and the hypothesis must fall to the ground as soon as it is proved that the Analschläuche are in reality only modified nephridia opening into a proctodæum. In addition to the anatomical evidence favoring such an interpretation, Hatschek ('80, pp. 60–62) has recently advanced strong evidence from an embryological standpoint for believing that they are nephridia which primitively opened directly to the exterior.

Among the attempts to find a homologue of the segmental duct already present in the Worms may be mentioned the longitudinal canal described by Hatschek ('78, p. 117 *seq.*) in the larva of Polygordius. Were Hatschek's account accurate, it would doubtless warrant great changes in our conceptions of the interrelationships of the Vermian nephridia, and of the origin of the Vertebrate kidneys; but his statements have not been confirmed by any subsequent observations, though several investigators have concerned themselves with this interesting form (Fraipont, '87, p. 83; Eisig, '87, p. 662; E. Meyer, '87, p. 594; Bergh, '85, p. 27, footnote).

The remaining views in respect to the nature of the duct agree in regarding it as a secondary growth.[1] Beard ('87, p. 651) and Haddon ('87) accept the ectodermal origin of the segmental duct, and endeavor to give it phylogenetic significance by assuming that the ontogenetic connection of the duct with the ectoderm indicates that it was represented in the phylogeny at first by a groove into which the nephridia opened, and that this groove gradually became closed and was cut off as a tube extending from the most anterior tubule backwards to the cloaca. Rückert ('88) and van Wijhe ('89, pp. 507, 508), on the other hand, assert a gradual backward growth of a primitively anterior opening.

None of these views are compatible with the fact that in many Vertebrates the duct is demonstrably of mesodermal origin. They also seem to me to give insufficient significance to the mode in which the pronephric diverticula unite to form a longitudinal canal; and the first two authors neglect it wholly.

Finally, the abandoned view of Balfour ('76, pp. 25, 26), according to which *the duct arises by the fusion of the distal ends of the several nephridia*, has been revived by Eisig ('87, p. 649), and was accepted by Rückert ('88, p. 264) for the *pronephric portion* of the duct. This view seems to me much the most probable, and I am inclined to accept it.

[1] Here belongs also the view of Boveri ('90), which has already been discussed (page 265).

In the foregoing discussion, I have endeavored to show that there is considerable evidence in favor of the view that the excretory system of Vertebrates has developed from a system of metameric nephridia, such as are present in Annelids. None of the evidence seems to me, however, final. The excretory systems of the two groups are very similar, but we have no means of limiting definitely the part that has been played by physiologically similar needs in moulding the structure of the organs. Nor am I committed to the theory of the Annelidan extraction of Vertebrates. I fully realize that such a theory can only be established by investigations which shall include in their scope the entire organization of the two groups. So far as this larger theory has been dealt with in this discussion, it has been with the view of contributing such evidence as the excretory system offers, and I have naturally left untouched the mass of evidence which proceeds from other organs. To this in addition we must appeal for the justification of the broader theory.

Cambridge, April 25, 1891.

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EXPLANATION OF FIGURES.

All the Figures, unless otherwise stated, were drawn with the aid of an Abbé camera lucida, and represent the appearance of the *anterior* faces of the sections. Plates I.–IV. were made from preparations of Rana sylvatica Le Conte; Plates V.–VIII. from Rana sylvatica Le Conte, Bufo americanus Le Conte, and Amblystoma punctatum Linn.

ABBREVIATIONS.

(For the meaning of letters *a*, *b*, *c*, *d*, *e*, *f*, in Figures 24–26, see the explanation of those Figures.)

ao.	Aorta.
can. comn.	Communicating canal.
cd. spi.	Spinal cord.
cl. ms'drm.	Mesodermal cells.
cl. vt.	Yolk cells.
cl.	Cloaca.
cœl.	Cœlom.
cœl.'	Protovertebral cavity.
cœl.''	Body cavity.
cp. sng.	Blood cells.
cps. pr'nph.	Pronephric capsule.
cras. gn.	Ganglionic thickening.
cras. pr'nph.	Pronephric thickening.
cras. so'plu.	Somatopleural thickening.
d.	Dorsal aspect.
dt. sg.	Segmental duct.
dt. Cuv.	Ductus Cuvieri.
dx.	Right side.
ec'drm.	Ectoderm.
ec'drm.'	Superficial layer of same.
ec'drm.''	Deep layer of ectoderm.
en'th.	Endothelium.
fnd. arc. vr.	Deep layer of a vertebral arch.
fnd. cps.	Fundament of the pronephric capsule.
fnd. dt. sg.	Fundament of the segmental duct.
fnd. glm.	Fundament of the glomus.
fnd. glm.'	Fundament of glomerulus.
fnd. gn. spi.	Fundament of a spinal ganglion.
fnd. mbm.	Limb bud.
fnd. ms'nph.	Fundaments of mesonephric tubules.
fnd. nph'st.^{I}	Fundament of first pronephric nephrostome.
fnd. pul.	Lung bud.
glm.	Glomus.
gn. nd.	Ganglion nodosum.
gn. spi.	Spinal ganglion.
hp.	Liver.
in.	Intestine.
la. l.	Lateral plate.
la. med.	Medullary plate.
la. ms'drm.	Mesodermal plate.
la. pi'ton.	Peritoneal layer.
la. pr'vr.	Protovertebral plate.
la. so.	Somatic layer.
la. spl.	Splanchnic layer.
m.	Median.
mb. ba.	Basement membrane.
ms'drm.	Mesoderm.
ms'chy.	Mesenchyme.
my'tm.	Myotome.
n. l.	Nervus lateralis.
n'cd.	Chorda dorsalis.
nph'stm.	Nephrostome.
nph'stm.$^{I., II., III.}$	1st, 2d, and 3d pronephric nephrostome, respectively.
pi'ton.	Peritoneum.
pr'vr.	Protovertebra.
rx. ao.	Aortic root.
rx. vag.	Root of the vagus nerve.
sb.-n'cd.	Sub-notochordal rod.
sn. sng.	Blood sinus.
so.$^{I., II.}$ etc.	Somites I., II., etc.
so'plu.	Somatopleure.
sph. vt.	Yolk spherules.
spl'plu.	Splanchnopleure.
tbl. nph'stm.$^{I., II., III.}$	1st, 2d, and 3d nephrostomal tubules respectively.
tbl. pr'nph.	Pronephric tubule.
trn. clg.	Collecting trunk.
trn. com.	Common trunk.
va. sng.	Blood-vessel.
vn. crd.	Posterior cardinal vein.
vn. jgl.	Jugular vein.

PLATE I.

Fig. 1. A portion of a cross section through the anterior trunk region of one of the older embryos included under Stage I. × 110.

" 2. A cross section through the same embryo in the middle trunk region. × 25.

" 3. A portion of a cross section through the middle trunk region of one of the younger embryos in Stage I. × 92.

" 4. A portion of a cross section through the hinder trunk region of one of the younger embryos belonging to Stage II. × 92.

" 5. A portion of a cross section through the anterior trunk region of one of the older embryos from Stage II. The section passes through an interprotovertebral septum. × 110.

" 6. A portion of a cross section from one of the older embryos in Stage III. The plane of the section passes through the middle of Somite III. × 110.

" 7. A small segment of a cross section through the embryo shown in Figures 15–17 of Plate II. The Figure represents a portion of the ventro-lateral ectoderm with three subjacent mesodermal cells. × 615.

" 8. A portion of a cross section through the embryo shown in Figures 18–22, Plate III. It shows the fundament of the glomus. × 110.

" 9. A portion of a cross section through a slightly older embryo, showing the glomus in a more advanced stage of development. × 110.

" 10. A portion of a cross section through an embryo of Stage V., showing a branch of the aorta which gives off a small vessel to the glomus. × 150.

PLATE II.

All the Figures on this plate are magnified 110 diameters.

Figs 11 and 12. Portions of two frontal sections through the pronephric thickening of one of the older embryos belonging to Stage III.

Fig. 11 shows the dorsal margin of the thickening.

Fig. 12 shows a section through the nephrostomal region.

Figs. 13 and 14. Portions of two frontal sections from one of the younger embryos of Stage II.

Fig. 13 shows the ventral ends of the anterior protovertebræ.

Fig. 14 shows a section through the dorsal portion of the pronephric thickening.

Figs. 15–17. Portions of three cross sections through one of the younger embryos of Stage III.

Fig. 15 shows the anterior end of the pronephric thickening. The plane of the section passes a little behind the middle of Somite II.

Fig. 16 shows the pronephric thickening in the region of Somite V.

Fig. 17 shows the thickening near its posterior termination.

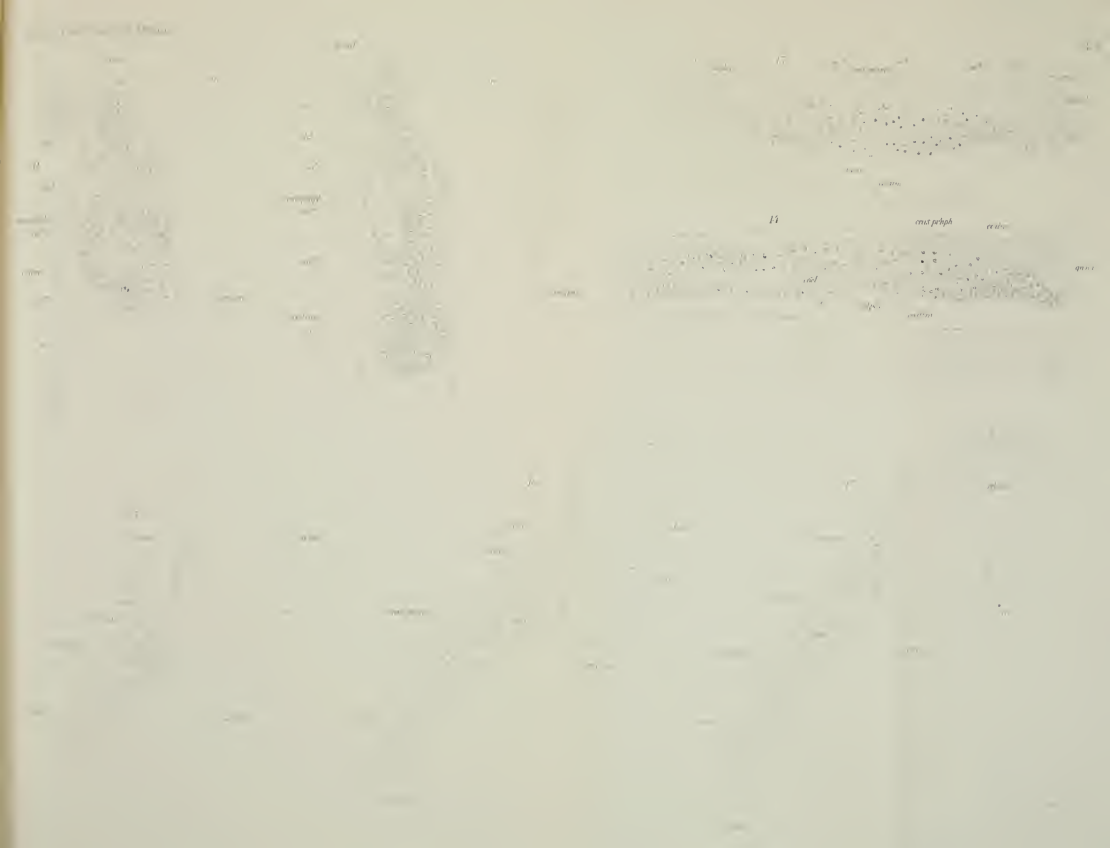


PLATE III.

Figures 18–22 and 27 are magnified 110 diameters; Figures 23–26, 260 diameters.

Figs. 18–22 Portions of a series of cross sections through an embryo of Stage IV. In Figure 18, the pronephros of the right side is shown; in the remaining Figures, the pronephric organs of the left side. The location of the several sections on the reconstruction (Fig. 39) is shown by the series of lines bearing corresponding numbers.

Fig. 18 shows the first nephrostome.

Fig. 19 is from a region between the first and the second nephrostomes.

Fig. 20 shows the second nephrostome.

Fig. 21 shows the third nephrostome and the anterior portion of the segmental duct.

Fig. 22 shows the segmental duct in the middle trunk region.

Figs. 23–26. Cross sections of the fundament of the segmental duct near its posterior termination, from an embryo of Stage IV.

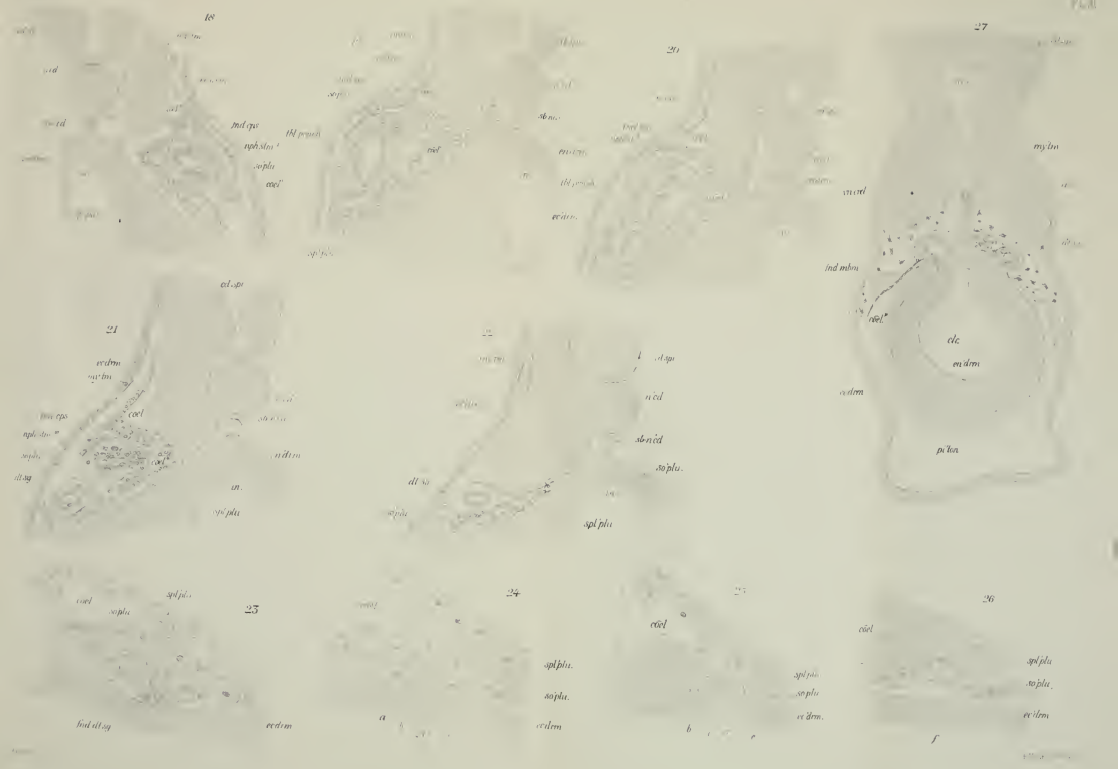
Fig. 23 shows the duct five sections in front of its termination.

Fig. 24, three sections before its termination; *a.*, *b.*, and *c.*, cells in the fundament of the duct; *cd.*, portions of the two cells *c.* and *d.*, which are to be seen in the following section.

Fig. 25 shows the duct one section in front of its termination; *c.* and *d.*, cells in the rudiment of the duct; *b.* and *c.*, portions of two cells bearing the same lettering in Figure 24.

Fig. 26 shows the depression of the somatopleure (*f.*) directly behind the tip of the fundament of the duct.

Fig. 27. A cross section from a larva whose pronephros is shown in Figure 41. It shows the opening of the segmental duct into the cloaca.


16
ind.qu
ind.qu
ect.pt
ect.pt
sph.sfen
sq.pa
ect
ect.pt
spl.pla
20
sph.sfen
ect
ect.pt
ect.pt
27
myl.fm
ind.mfm
ect.pt
clc
en.drm
ect.drm
pt.fen
21
ect.sq
ect.drm
sq.fm
ect
ect.pt
sph.sfen
sq.pa
n.dr.m
an.
spl.pla
22
ect.sq
n.ect
sph.ect
sq.pla.
dl.sq
spl.pla
23
ect
sq.pa.
spl.pla.
ind.dl.sq
ect.drm
24
ect.pt
spl.pla.
sq.pla.
a
ect.drm
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ect.drm.
b
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ect.pt
spl.pla
sq.pla.
ect.drm
f

PLATE IV.

Fig. 28. Part of a cross section through the anterior trunk region of a larva belonging to Stage VI. The Figure shows the pronephros in the region of the first nephrostome. × 110.

Fig. 29. Part of an oblique longitudinal section through a larva of Stage IV. The plane of the section was directed so as to cut the somatopleure tangentially along the line of the three nephrostomes. Its direction is represented by the line 40 in Figure 20. × 110.

Fig. 30. Part of a cross section through the middle trunk region of a larva, from which Figure 28 was also drawn. (Stage VI.) × 110.

Fig. 31–38. A series of diagrams illustrating the convolution of the pronephric tubules. These diagrams, which are based upon reconstructions from cross sections, merely serve to show the number and approximate location of the loops in a longitudinal direction. No attempt has been made to indicate in the diagrams the changes in position undergone by the tubules in a transverse direction. The gray tint represents the common trunk and the anterior portion of the segmental duct. The first nephrostomal tubule and the collecting trunk are colored pink. The second and third tubules are represented in yellow and orange respectively.

Figs. 31–34 are from various larvæ of Stage V.

Fig. 32 is a diagram of the reconstruction shown in Figure 40.

Figs 33 and 34 represent the right and the left pronephros respectively of the same individual.

Figs. 35–37 are from various larvæ of Stage VI.

Fig. 36 is a diagram of the reconstruction shown in Figure 41.

Fig. 38 is from a larva of Rana halesina.

Figs. 39–41. A series of reconstructions from cross sections of larvæ in different stages of development. In Figures 40 and 41, the common trunk and the anterior portion of the segmental duct have been shaded without color; the collecting trunk and the first nephrostomal tubule have been colored pink; and the second and third nephrostomal tubules are respectively yellow and orange. × 65.

Fig. 39. Right pronephric pouch of a larva belonging to Stage IV., viewed from the median side. The ×'s represent the position of the nephrostomes. The lines 18–21 show the various levels at which the sections represented in Figures 18–21 were made.

Fig. 40. Right pronephros of a larva belonging to Stage V., viewed from the median side.

Fig. 41. Right pronephros of a larva belonging to Stage VI., viewed from the ventral side, the external face being uppermost.

PLATE V.

Fig. 42. A portion of a cross section through the anterior trunk region of a larva of Bufo, belonging to Stage V. The Figure shows the pronephros in the region of the first nephrostome. × 110.

Fig. 43. A section through the rudiment of the duct near its hinder tip, from an embryo of Bufo belonging to Stage IV. × 500. Zeiss apochr. 4 mm. Oc. B.

Fig. 44. A portion of a cross section through the anterior trunk region of an embryo of Amblystoma belonging to Stage III. The section shows the pronephric thickening in the region of its greatest development. × 65.

Fig. 45. A portion of a cross section through the anterior trunk region of an embryo of Rana belonging to Stage IV. The section shows the pronephric pouch in the region of the second nephrostome. × 110.

Fig. 46. An embryonic blood corpuscle occurring in the glomus of a larva of Bufo belonging to Stage V. × 955.

PLATE VI.

Fig. 47. A portion of a cross section through the anterior trunk region of a larva of Bufo belonging to Stage V. The Figure shows the pronephric structures in a region between the first and second nephrostomes. × 158.

Fig. 48. A portion of a cross section through the middle trunk region of an embryo of Amblystoma belonging to Stage I. × 65.

Fig. 49. Anterior face of a cross section through the glomus of a larva of Bufo belonging to Stage V. × 470. Zeiss apocr. 4 mm. Oc. 6.

Fig. 50. Anterior face of a portion of a cross section through the right glomus of the same larva, including also the opposite peritoneal wall. × 710. Zeiss apochr. 4 mm. - Oc. 12.

Fig. 51. A cross section (right side, anterior face) through the pronephros represented in Figure 37. The section passes directly in front of the third nephrostome, and shows the expanded region of the common trunk at the level of its union with the collecting trunk. × 90.

Fig. 52. A portion of a cross section through the glomus of a larva of Bufo belonging to Stage V. The Figure shows an infolding (opposite the letters *cœl.*″) of the outer peritoneal layer of the glomus. × 500.

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PLATE VII.

Fig. 53. A portion of a cross section through the posterior trunk region of a larva of Amblystoma belonging to Stage VI. The section shows the fundament of the second primary mesonephric tubule (*dt. sp.*). × 90.

Fig. 54. A portion of a cross section through the middle trunk region of a larva of Amblystoma belonging to Stage VI. The section shows one of the "cords of cells" which occur between the mesonephros and the pronephros; it exhibits a case of nuclear mitosis in the peritoneum, which suggests the origin of these cells. × 500. Zeiss apochr. 4 mm. Oc. 8.

Fig. 55. A portion of a cross section through the anterior trunk region of an embryo of Amblystoma belonging to Stage III. The pronephric thickening is shown in the region of the middle of Somite II. × 90.

Fig. 56. A portion of a cross section from the same series. The pronephric thickening is shown in the region of the posterior face of Somite II. × 90.

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vn.crd.
en
endrm

PLATE VIII.

Figs. 57–60. Reconstructions of several pronephridia of Amblystoma larvæ belonging to Stage V.

Fig. 57. Reconstruction of a pronephros showing three nephrostomal tubules.

Figs. 61–65. Reconstructions of several pronephridia of Amblystoma larvæ belonging to Stage VI.

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